AN

INTRODUCTION TO

THE SCIENCE OF BOTANY

Basic Botany

By

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SECOND EDITION

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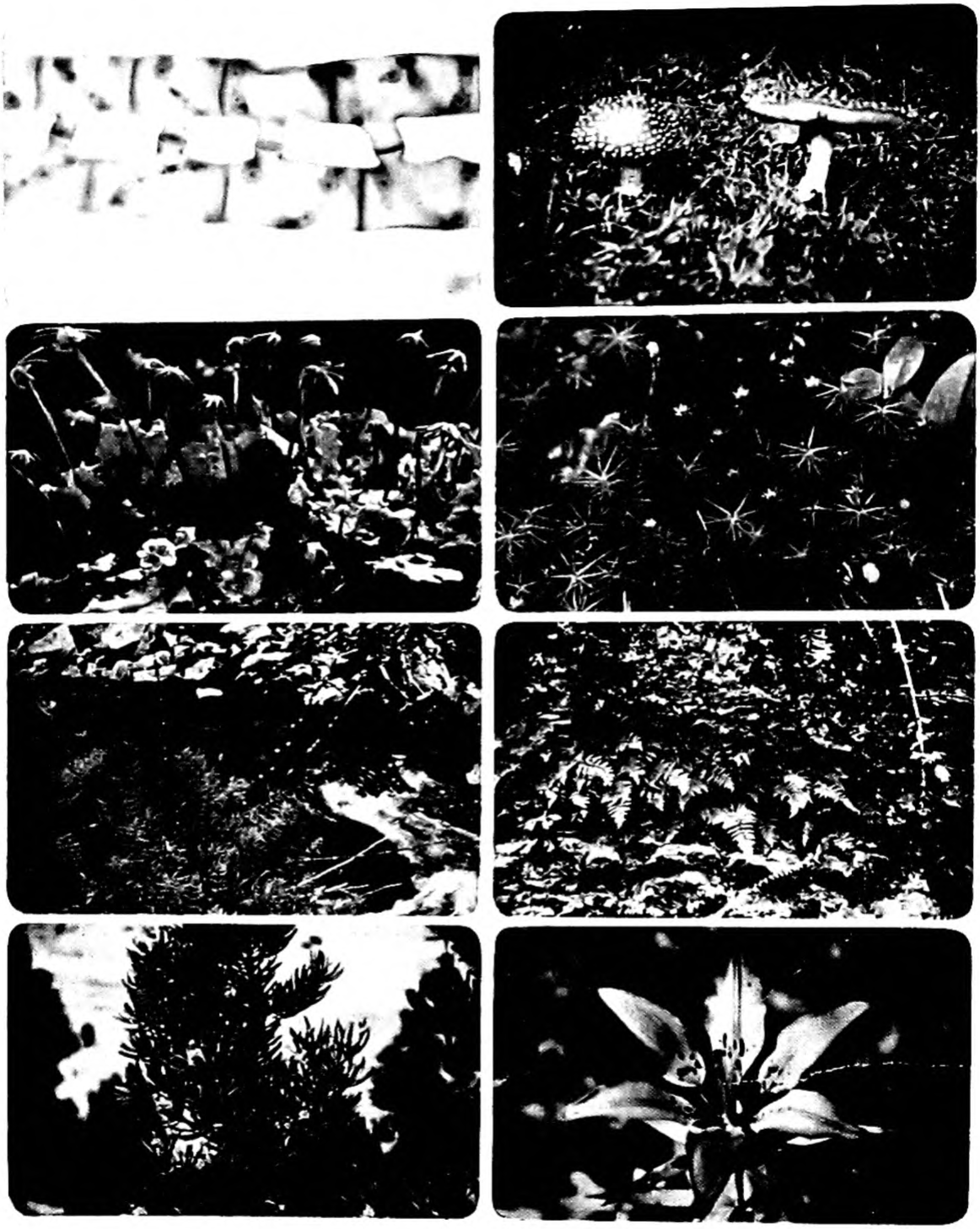

REPRESENTATIVES OF THE PLANT GROUPS

Spirogyra (Alga)
(Photomicrograph by T. H. Holmes)

Marchantia (Liverwort)

Equisetum (Horsetail)

Pinus (Gymnosperm)

Amanita (Fungus)

Polytrichum (Moss)
(Courtesy, George Lower)

Cystopteris (Moss)

Lilium (Angiosperm)
(Courtesy, Turtox Co.)

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To my students
who have supplied the stimulus
for the preparation of this book

Preface to Second Edition

Some five years have passed since the preface to the first edition of *Basic Botany* was prepared. Now an entirely new generation of students occupies classrooms and laboratories. Nevertheless, the problems of teaching and learning remain unchanged. The symbolism used in the earlier preface continues to be sound. Adjustments of the microscope and the materials available for use are being improved, but the human mind continues to function as before.

New techniques in the use of the electron microscope and the development of the phase microscope have added important tools to the equipment of the investigator. Much progress in the gathering of facts is being made constantly at the research level, and much newly acquired information is slowly influencing interpretations. Biochemistry with its offspring, enzymology has been shedding new light upon almost every phase of life activity. While perhaps less spectacular, genetics, cytology, and paleontology are all affecting and being affected by all the other disciplines.

Published reports by numerous individual investigators and research teams, and those of symposia, together with reviews and compilations by specialists have assembled great masses of growing information.

Use of *Basic Botany* as a textbook by many students and teachers has made obvious a great number of needed changes of expression and lacks of content. In so far as possible, these have been corrected here.

Special care has been taken to impress the student with the fact of growth in knowledge on the part of scientists down through the centuries. In other words, much attention has been given to the historical development of both equipment and ideas.

As a guide to that important student who has the urge to delve deeper into the subject matter of the various chapters, a small selected list of helpful references is included as "Supplementary Readings," at the end of each chapter, and a much more inclusive list of references is added beginning on p. 387.

The general outline found successful in the first edition is followed here. As subject matter permits, in this revision a somewhat greater stress is placed upon such applications to farm and garden as those of growth-regulating substances, vitamins, the micro-nutrients, enzymes and soil-water-mineral-nutrient relationships.

Acknowledgments are due to the editorial and production staffs of the Blakiston Company and to those users of the first edition who have spent much time and effort in preparing and submitting detailed constructive criticisms. Where material or illustrations have been borrowed directly from any source, proper citation is made at the point where the item is used.

FRED W. EMERSON

Winter, 1953

Preface to First Edition

A beginning student in the laboratory is learning to adjust his microscope. He turns his mirror until he has a clear white light; he mounts a small green object on a clean slide and places this on the stage; he sees only a greenish blur; he moves the coarse adjustment; the low-power objective begins to focus; and then, he sees something that is entirely new to him.

The experiences of this young student rather closely parallel the history of botany. Classification, structure, the various life activities, and numerous significant but seemingly unrelated observations have been like the various rays of light that first reached this student's eye: they held the attention but were not clearly in focus; their meaning was apparent only in part.

In the field of botany and in biology in general the focus has been sharpening until at present all these dimly perceived parts are seen to be the phases of a single unit. This unit is protoplasm, the activities of which constitute what we call life. The various functions or life activities are determined by differences in physicochemical organization, and both structure and functioning are controlled by the genes, influenced by environment.

This book has been written from such a unified point of view. Physiology, anatomy, morphology, taxonomy, genetics, and ecology are all included but not in an altogether traditional order. Leaves, stems, and roots are discussed in rather full detail, but as integral parts of the plant, which is a functional as well as a morphologic unit.

The author hopes that his treatment of the subject will fill in a unique way the requirements of a considerable number of college students and will advance both the botanical and the pedagogic theory of many teachers.

The plan and content have been determined by the experience of the author, who has taught and carried on research in a rather wide range of educational institutions and climatic conditions. As far as possible, living plants, especially those with which the student is likely to be familiar, have been selected as illustrative material. When it has been necessary to refer to exotic or little-known species for the sake of completeness, a special effort has been made to make these forms as real as possible to the student.

Emphasis has been placed upon the scientific method of solving problems. The occasional questions scattered throughout the text are intended to cause the student to summarize his growing knowledge and to draw tentative conclusions from assembled facts. When the more direct presentation of information has seemed best, some attention has usually been given to the methods by which this knowledge has been obtained.

The underlying meaning of the facts and principles under discussion has been continually emphasized. The conviction has been constantly in mind that both students and teachers learn, study, and investigate under the drive of significance. Freshness and spontaneity of work come gradually to characterize the atmosphere of classroom and laboratory when these are made places in which students are led from present knowledge to facts unknown to them, in ever-widening circles; when they are made to realize the significance of the work at hand; and when they discover their own powers of mastery over themselves and nature by means of the tools of science. Under these conditions facts are grasped in natural settings, and a healthy independence in thought and procedure results. If this book helps some students and teachers better to coöperate to these ends, it will have fulfilled the purpose for which it was written.

The author is greatly indebted to many persons for general and specific aid in the preparation of the manuscript and the illustrations. Where material has been borrowed directly from any source, proper citation is made at the point at which the item is used. The greatest debt of all is due the hundreds of students who have provided the stimulus and offered the criticisms that have helped to shape the content of this book. Special mention should be made of Mrs. Pauline Merrill McCleary and Mrs. Tillie C de Baca, both of whom have contributed parts or all of many of the drawings.

FRED W. EMERSON

Contents

Chapter 1

INTRODUCTION: PLANTS AND SCIENCE

The Corn Belt of the Upper Mississippi Valley is now producing almost one-fourth more corn per year than could be raised on the same land up to about 1937. Not only is the yield greater but there are several improvements in quality as well. The following comparison of the past with the present should make these contrasts clear. In those earlier times some of the stalks grew to be tall while others near them were small and stunted; some of the ears were large and heavy with grains, others were only of fair size, and still others were so small and so poorly developed that they were not worth harvesting; some ears grew very low on the stalk, others at a height convenient to gather, and a few were higher than a man's head. Uniformity was rare and great variation was the rule only a few years ago. But now, examination of corn in the same region reveals stalks that are very sturdy and almost alike in height and size; ears that are uniform and at the right distance from the ground to be harvested easily; and grains that are of excellent size, form, and texture.

The explanation of this great improvement is not far to seek. Farm machinery and methods of caring for the fields have improved but the greatest difference is in the corn itself. Scientific investigations in recent years have advanced our knowledge of heredity in corn, as in almost all other living things. As a result of applying this new knowledge the modern farmer is now growing much more grain on a given area than he was able to produce less than a quarter of a century ago. At that time he had no way of choosing his seed corn except by relying on his own judgment and by saving for seed those ears which best met his standards. By way of contrast, the present-day farmer buys hybrid seed corn which has been expertly crossed by scientific specialists to combine the most desirable characteristics and to produce a high uniform yield and quality.

This is only one of a long and rapidly extending list of examples that illustrate ways in which increasing scientific knowledge is being applied to the solution of problems and the supplying of needs. The successful growing of any kind of crop, the proper care of orchards, the management of grazing lands, the maintenance of forests, the propagation of ornamentals, or the keeping of a potted plant in a window, all require the application of botanical principles. The more completely these principles are understood, the better the prospect of success.

BOTANY, A BRANCH OF SCIENCE

Botany may be defined as that branch of science which deals with plants. The word science is derived from the Latin word *scire*, which means *to know*. But, to quote a great scholar of the generation just past, "we know nothing until we can find it out." Science means, then, not only knowledge but discovery; and every real scientist is an investigator—a searcher for knowledge.

Facts, once found out, can often be used in making still other discoveries, and can also be applied to the meeting of human needs. A case in point is that of the hybrid corn described above. At about the beginning of the present century, when the basic principles of heredity first came to be under-

stood, this new knowledge laid bare a great array of unsolved problems. As discovery succeeded discovery, each opened new vistas of the unknown, until in our day investigators are dealing with questions that would have seemed fantastic only a generation ago. And the end is not yet, for new tools of research are being invented continually.

Early in this century, while still searching for the fundamental laws of heredity, botanists soon came to realize that field corn could be used to advantage in their studies. Some of their findings suggested ways by which yields might be greatly increased. Now those same principles are applied to the large-scale production of hybrid corn. It is important to recognize that the discovery of primary laws preceded their practical application. Not only in this but in every phase of science the discovery of basic principles must always come first; then applications may or may not be found. Almost every investigator is likely to be confronted from time to time by questioners who doubt the value of such experimentation. Often the inference is strong that the search for facts that are not clearly useful is a waste of time. Such a question only betrays a common misunderstanding of the scientist and his work. His work is first of all discovery, and it is impossible to foresee the economic value or lack of it of any given fact before it is found out. The finding of scientific principles and the formulation of fundamental theories is often called *basic* or *fundamental research*, and the application of these principles to human use is *applied science*. Each depends on the other and both are necessary for human welfare.

How Scientists Work. Modern scientific methods, like present-day art, literature, architecture, and in fact all kinds of human endeavor, have their roots in the past. In one way, however, science stands a little apart from the rest in that science is more completely a product of human curiosity. The earliest written records of man's thoughts show that people were already trying to interpret and explain their surroundings and experiences. The sun, the changing moon, day and night, the sequence of the seasons, storms, dreams, hunger, cold, sickness, and death all wove themselves into a pattern that affected all of life. Early primitive attempts to explain these experiences led to myths and legends without end. Folklore and superstition became deeply entrenched through the generations and few dared to doubt the beliefs of the clan. But the very same curiosity and desire to understand that led to these mistaken interpretations also brought about the slow development of better ways to arrive at truth.

During the period from the fifth to the third centuries B.C. the Greek philosophers were breaking away from mythology, substituting hypotheses and conjecture of a high order. Even so, these great thinkers seem never to have discovered that experimentation could be used to test the validity of ideas. They guessed remarkably well, though by no means perfectly, and accepted their untried hypotheses as final statements of fact.

So great did their influence become that for many centuries the intellectual world clung to traditions that grew up around their early philosophical writings. Even as late as the Middle Ages questions of fact were decided by referring to the classics. Thus a medieval scholar who saw sunspots decided that he was mistaken because Aristotle had inadvertently mentioned "the immaculate (spotless) face of the sun." Although those ancient philosophers had broken with the superstitions that were old in their time, their words became a creed that might not be questioned by later generations. Almost endless debates were sometimes carried on over the meaning of the words used by some earlier thinker.

In 1612 Francis Bacon, in revolt against these sterile mental exercises, published his "New Methodology" in which he formulated an outline of systematic observation and experiment, thus laying the foundation for modern scientific investigation. Although he made little use of the revolutionary methods he proposed, others gradually learned to follow his lead, and the growth of research based on critically evaluated, carefully collected data ensued. At long last man's search for knowledge was reaching a higher level.

Under the impact of this new approach, the authority of tradition began to give way. Experience soon convinced investigators that every effect results from one or more measurable causes.

Therefore the discovery and measuring of these causes became the primary objective, and everywhere *cause and effect relationships* were being discovered. In such an atmosphere superstitions cannot long persist. Thunderbolts, which had been explained for ages as the acts of angry deities, were shown to be but electric discharges. Diseases ceased to be interpreted as actions of evil spirits. A new outlook on life was emerging. Man was beginning to understand and therefore to control his environment. Such were the early steps leading to the ever-widening scope of modern scientific research. While the various subjects for investigation require somewhat different methods of attack, there are a few steps that are almost always taken.

First, the problem is clearly outlined.

Second, all possible information that has a bearing on it is assembled. To this end, the investigator both searches for all relevant discoveries that have been made by others and carries out carefully planned observations and experiments of his own. Errors of all kinds must be avoided, for these can lead to seriously incorrect conclusions. One of the most important means of securing reliable facts is the *control experiment*. This type of investigation is set up in two parts. The *control* is carried out in a carefully arranged group of standard conditions such as of light, humidity, and temperature and the *experiment* duplicates all features of the control with the exception of the one factor being investigated. Thus, if the effect of light is being studied as it relates to some plant, the only difference between the control and the experiment will be that the experiment is carried out in light and the control in darkness. The contrasting results are recorded with great precision.

Third, all the evidence at hand is evaluated to see if a *theory* cannot be formed that will show agreement between the various facts.

Fourth, this theory is tested in every way possible to discover flaws. So long as discrepancies are not found, it stands; but if any appear, it is either amended or discarded.

This is a laborious method of discovery, but it has proved to be the most reliable way humanity has to gain new knowledge.

Scientific investigations deal with both nonliving and living things. Therefore there are such *Physical Sciences* as Physics, Chemistry, Geology, and Astronomy, with many subdivisions of each, and *Life Sciences*, often known collectively as *Biology*. The part of biology that deals with animals is *Zoology* while the part that deals with plants is *Botany*. The following brief outline indicates the differences in subject matter between these various branches of science. On the other hand, it does not show the important fact that all, or almost all, interlock with one another. As examples, new chemical elements are being created in the study of nuclear physics; fossils belong both to geology and to biology; and botany and zoology merge in certain organisms that are not distinctly either plants or animals.

Science:
- *Physical Sciences:*
  - *Physics:* Mechanics, electricity, etc.
  - *Chemistry:* Substances and their transformations.
  - *Geology:* The earth.
  - *Astronomy:* Planets, stars, galaxies, etc.
- *Biology:*
  - *Zoology:* Animals.
  - *Botany:* Plants.

Since the primary interest in this book is centered on plants, the various subdivisions of the science of botany are to be discussed in succeeding paragraphs.

The Many Phases of Botany. A casual examination of a forest or of a meadow in summer may leave one with the impression that all is uniform, quiet, and unchanging. Nevertheless, this is illusion. These living plants are not at rest as they may appear, for activities almost without number are continually going forward. Water is entering roots from the soil, is playing many parts throughout the plant bodies, and much of it is evaporating into the air; roots are steadily driving their tips through the soil; new structures of many kinds are being built while old dead ones are being torn apart by the processes of decay; and food is being made, used, and destroyed.

These activities and many more, all of which are noiseless and invisible, are always behind the scenes in any landscape which includes living green plants.

Because of the myriad forces of many kinds which enter into the activities of plants in their life processes and which play upon them from without, the science of botany has numerous phases. Every kind of plant—the giant tree or the microscopic fungus growing in its bark, the delicate pond scum floating in water or the sturdy century plant of the desert with its roots imbedded in dry soil for many months of the year, or any of the thousands of other plants on land or in the sea—must carry on certain active processes if life is to continue. They must absorb water and minerals; they must acquire food; they must respire. These and similar activities associated with life constitute the subject matter of *plant physiology*.

But the plant in undisturbed nature must live in a complex world of change—a world of rain and drought, of heat and cold and, most complex and varied of all, a world of other living things, both plant and animal, some of which are helpful to it, while others tend to interfere with its welfare or even to destroy it. The study of the plant in its relation with its surroundings is the branch of botany known as *plant ecology*.

Like other living things, the plant is subject to disease. Various organisms finding lodgement in its tissues may cause more or less damage or even death. The study of these diseases and their control is commonly called *plant pathology*.

There are many thousands of kinds of plants, each with its own peculiarities and each with a name. The naming of plants is probably the oldest of all phases of botany, dating back to the dawn of history. At first it must have had little of the orderly nature of science. But, just as astrology preceded the science of astronomy, and alchemy developed into chemistry, so the rather aimless naming and classification of the most useful or noxious species has, through the centuries, become an important phase of organized knowledge which bears the name of *plant taxonomy* or *systematic botany*.

Plants and animals inherit characteristics from their ancestors. This fact leads to the study of *genetics*, the phase of biology that deals with heredity. But it is becoming more and more evident that certain orderly changes in the hereditary constitution of organisms take place from time to time as generation succeeds generation, slowly bringing about the development of new kinds. This process of modification through descent is called *evolution*.

The various kinds of plants have their own peculiar organization, the study of which is *structural botany* or *plant anatomy*.

Of the multitude of plants some are simple while others are complicated, some produce seeds and others do not, and in many other ways they fall readily into groups of individuals which have the same important sets of characteristics and peculiarities of organization and reproduction. The study of the form, structure, and stages in development of plants is called *plant morphology*.

When all kinds of plants are grouped together according to their morphologic characteristics, a convenient outline results. Numerous types of outlines have been developed, one of the simplest of which follows. This may be used as a background for the time being until it is possible, later in this course, to develop a more effective one (p. 185; Chapters 12–21).

The Plant Kingdom:

- Thallophytes
  - Algae
  - Fungi
  - Lichens
- Bryophytes
- Pteridophytes
- Spermatophytes
  - Gymnosperms
  - Angiosperms
    - Monocotyledons
    - Dicotyledons

THALLOPHYTES. These are simple plants without true roots, stems, or leaves and without flowers or seeds. The entire plant may be only a single cell or a small group of cells, or it may be large with little specialization into different kinds of tissue. The reproductive structures are simple.

ALGAE. The algae are thallophytes that are able to manufacture food by means of a green substance called chlorophyll. Examples are fresh-water algae or pond scums and the red and brown seaweeds.

FUNGI. Fungi are thallophytes that do not have chlorophyll. This group includes such plants as mushrooms, molds, mildews, and bacteria.

LICHENS. These are thallophytes in which the plant body is constructed of an alga and a fungus growing together as if they were a unit.

BRYOPHYTES. The bryophytes are small plants without wood, flowers, or seeds but sometimes with slightly organized stems and leaves. True roots are never present although hairlike growths often attach the plants to the soil. Their mode of reproduction is more complicated than that of most of the thallophytes. These are the liverworts and mosses.

PTERIDOPHYTES. These are plants without flowers or seeds, but characteristically they have woody tissues, especially in stems and roots. This group includes ferns, horsetails, scouring rushes, and club mosses.

SPERMATOPHYTES. This group includes all the seed plants.

GYMNOSPERMS. These are trees and shrubs whose seeds are not encased in pods or other similar enclosures. Often the seeds are only attached to the scales of cones. Well known examples are pine trees, ginkgo, spruces, and firs.

ANGIOSPERMS. The angiosperms are plants with seeds enclosed in structures called ovary walls.

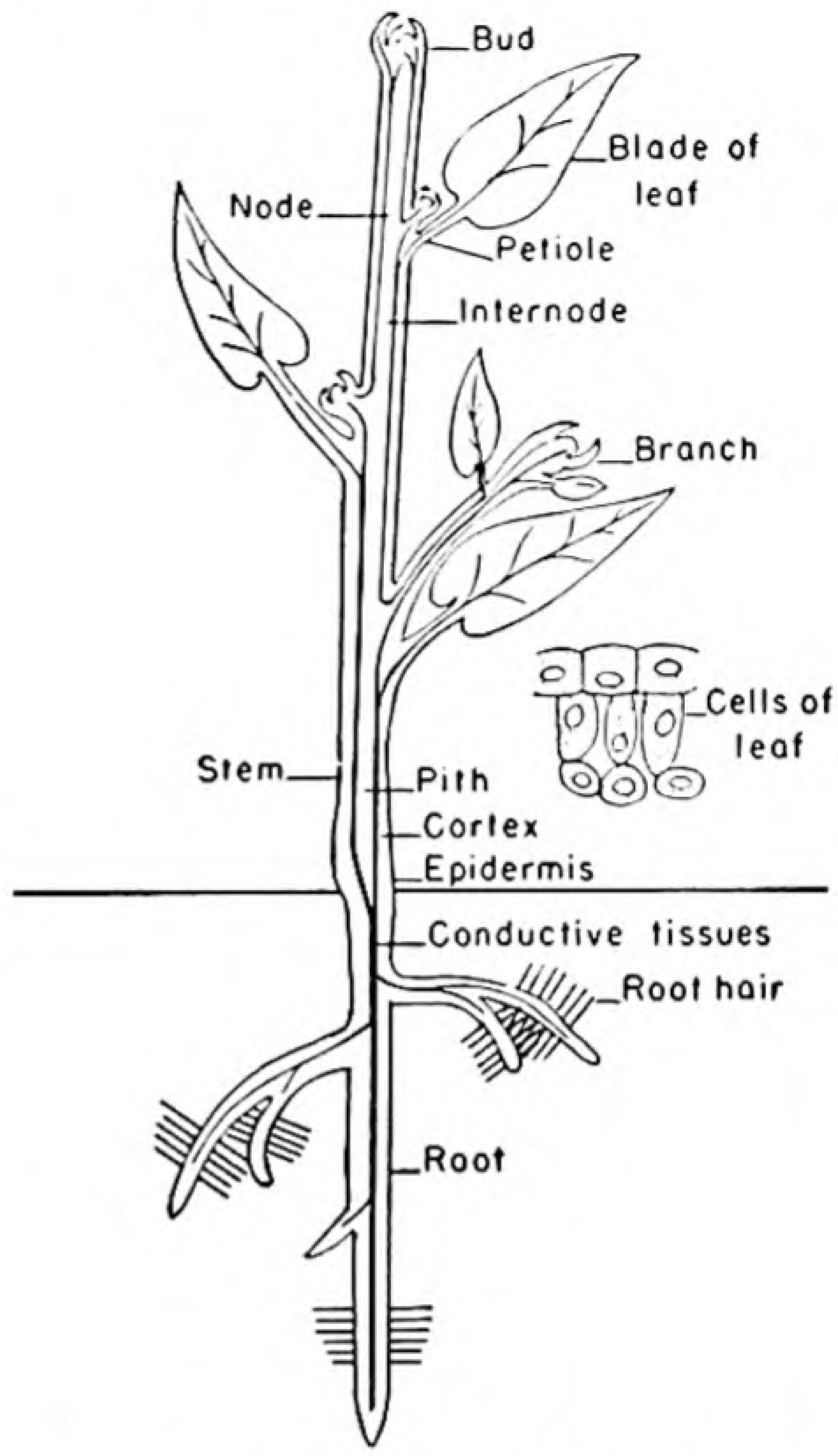
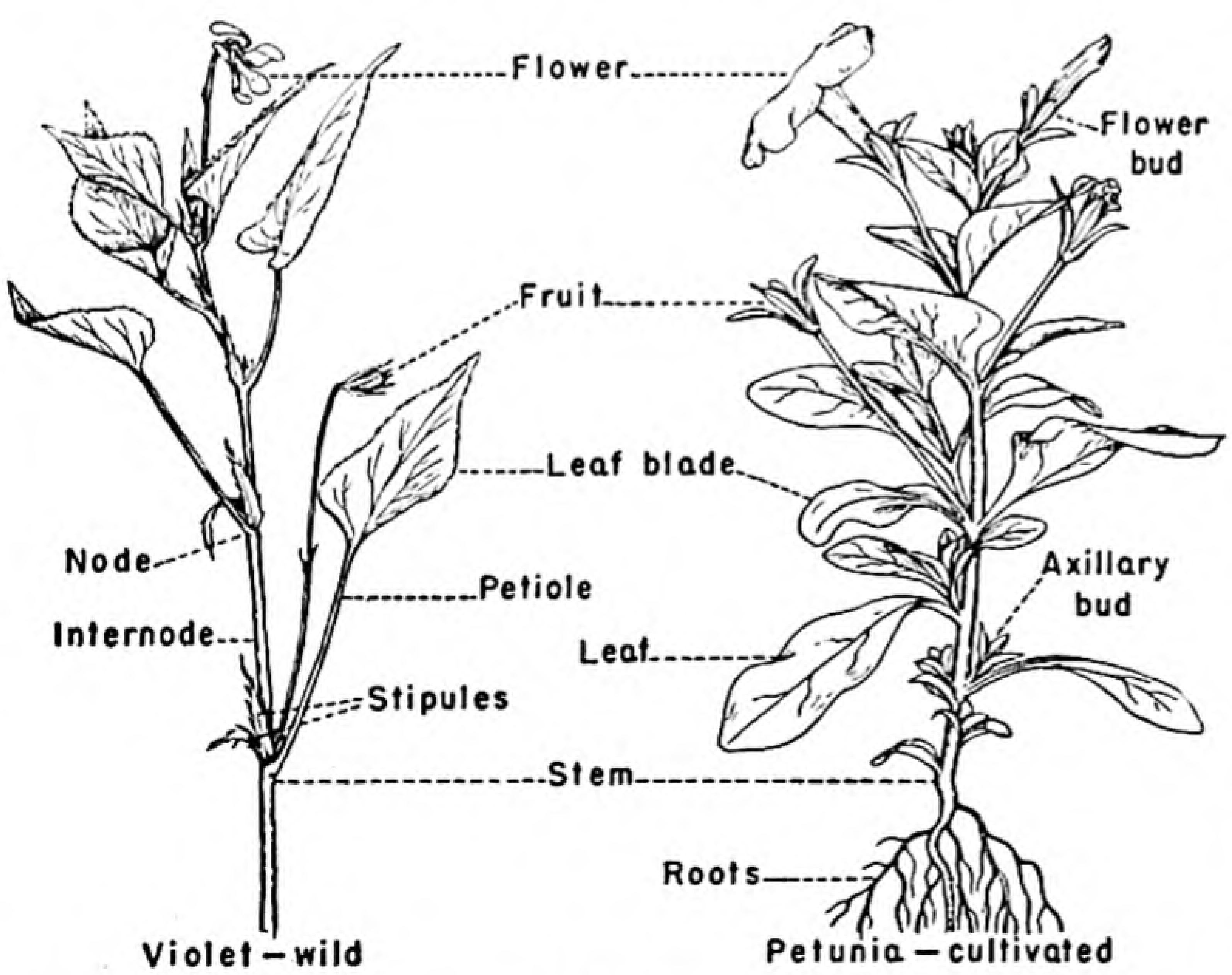


Diagram of plant, showing positions of internal structures. (Adapted from Eames and MacDaniels: "Introduction to Plant Anatomy.")

Monocotyledons. These are angiosperms with a single cotyledon or "seed leaf" in each seed. The leaves almost always have parallel veins. Such plants as corn, bamboo, sugar cane, grasses, palm trees, and lilies are good examples.

Dicotyledons. Dicotyledons are angiosperms with two cotyledons in each seed. The leaves almost always have netted veins. Well-known examples are beans, maples, geraniums, willows, and cotton.

Parts of Well-known Plants. Common cultivated plants and wildflowers are usually made up of roots, stems, and leaves, and at certain times they have flowers and fruits. The broad,



Parts of common plants. (*Left*) Wild violet. (*Right*) Cultivated petunia.

flattened part of a leaf is the *blade* and the slender support of the blade, when present, is called the *petiole* or *leafstalk*. Attached to the base of the petiole there are sometimes two small structures, the *stipules*. These growths are sometimes leaflike, as in the pea and violet; sometimes in the form of sharp spines, as in black locust; and sometimes tendrils that cling to supports, as in some species of *Smilax*.

The *roots* commonly grow downward from the base of the *stem*. The parts of the stem from which leaves and buds arise are called *nodes*, and those between the nodes are *internodes*.

The diagram of plant, on page 5, shows, in a much simplified form, the general arrangement of the structures that constitute the interior of a common seed plant. Later discussions will be devoted to these various parts. The leaf can be seen to be made up of many small bodies, the *cells*. While these are not shown in other parts of this diagram the entire plant is constructed of them. All the life activities of the plant are carried on by the protoplasm, the substance from which the cells are organized.

Chemical Foundations. Before life processes can be comprehended it is necessary to have a grasp of some of the basic ideas underlying chemistry. The reason is that all vital activities result from chemical changes which are continually in progress in living protoplasm.

All matter—whether it is solid, liquid or gaseous, living or nonliving—is composed of certain elementary substances known as *chemical elements*. A few that are somewhat familiar to everyone are aluminum, carbon, copper, gold, hydrogen, iron, lead, nitrogen, oxygen, phosphorus, radium, silver, and sulfur. The smallest possible particle of an element is called an *atom*. Occasionally an element occurs in almost pure form but practically always two or more are either mixed together or are combined into *compounds*. In a *mixture*, the substances may be intermingled in any proportion, e.g., the gases, oxygen and hydrogen, may be mixed together in any desired relative amounts. On the other hand, *chemical reaction* results when certain elements or groups of elements are brought together under appropriate conditions so that they unite to form something different from either of the original substances. To illustrate, if the two gases, oxygen and hydrogen, are mixed in a closed vessel they may be caused to unite to form water,

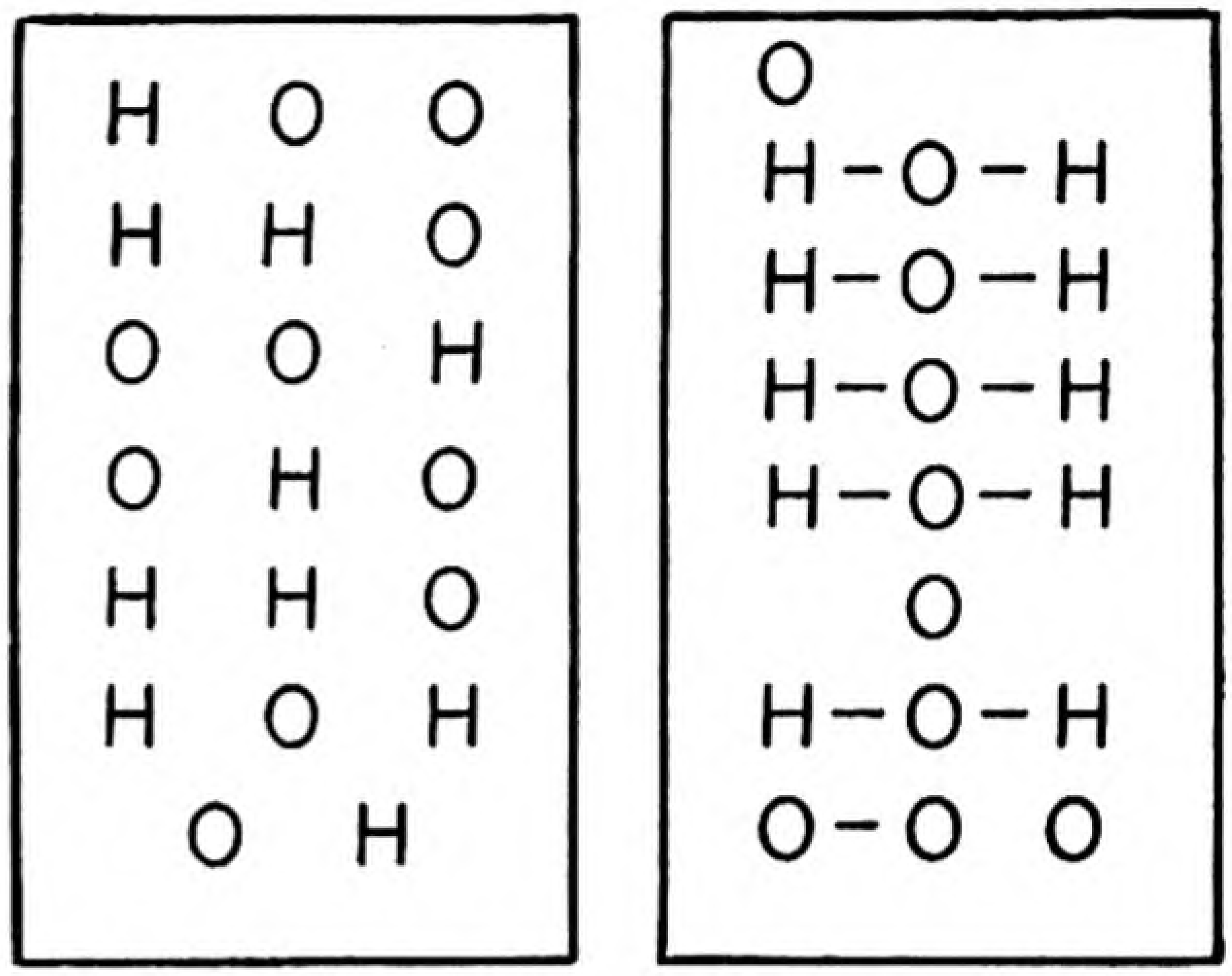


Diagram showing differences between mixtures and compounds. (*Left*) Mixture of equal numbers of atoms of hydrogen and oxygen. (*Right*) The same after a chemical reaction has taken place uniting oxygen and hydrogen, forming molecules of water, H–O–H. Note that some atoms of oxygen are left after all the hydrogen has been used up in the formation of water.

the chemical formula of which is H_2O, by discharging an electric spark in the mixture. These two gases do not unite in the indefinite proportions that happen to be present but in the ratio of two atoms of hydrogen with one atom of oxygen. Such a definite chemical grouping is a *compound*. In this case the compound, water, is made of the two elements, oxygen and hydrogen.

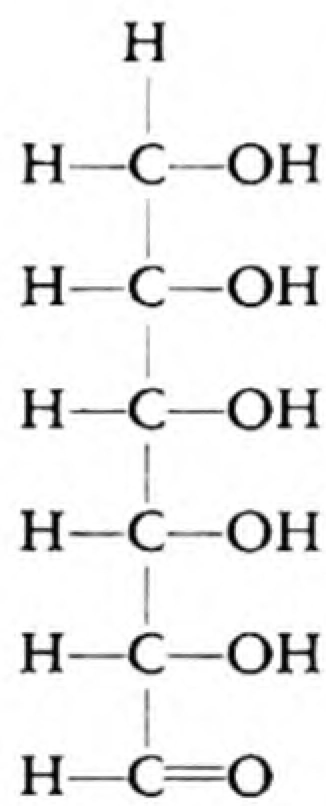
To restate and summarize, the smallest unit of an element is called an *atom*, and a chemical union of atoms forms a *molecule*. In other words, atoms are the units of elements; molecules are the units of compounds. In practice, an atom is usually represented by a symbol, as O for oxygen, H for hydrogen, C for carbon, etc., and a compound is expressed by a group of symbols. Thus water is made of two atoms of hydrogen (H_2) attached to one of oxygen (O) and the formula for a molecule of the compound is H_2O. In a similar way, carbon dioxide

is a compound, one molecule of which has two oxygen atoms (O_2) united with one atom of carbon, (C). The formula for one molecule of carbon dioxide is, therefore, CO_2. In this way a chemical formula indicates the composition, and to some degree the size and complexity, of the molecules of a compound. Atoms or small groups of atoms of certain compounds tend to *dissociate* or separate from one another when the compound is dissolved. Each of the separate parts takes on an electric charge and is now called an *ion*. Because of the reduced size of these particles as well as the electric attractions and repulsions, ions act in somewhat different ways from molecules.

In subsequent chapters the terms atom, element, molecule, compound, ion, and chemical reaction will be used without further explanation. The student should not pass on to further work without a clear understanding of these terms. For additional study any good college textbook of general chemistry, especially in the introductory chapters, should be helpful unless the student already has a grasp of elementary chemistry.

Inorganic and Organic Compounds. The foregoing examples represent a group of simple substances known as *inorganic compounds*. Almost all the materials absorbed by plants from the soil as well as many of the most familiar substances in common use such as table salt and baking soda are *inorganic compounds*. In contrast, most of the matter directly involved in life processes belongs to a group commonly called *organic compounds*. These are peculiar in that carbon atoms always hold key positions in them. No other element behaves quite like carbon in several respects. Its atoms are capable of uniting with each other and also with those of a number of other elements, forming extremely intricate molecules. These are far larger and more complex than those of any inorganic substance; and it is this very complexity, together with great capacity for change inherent in organic compounds, that makes life processes possible.

The composition of any compound may be expressed by a chemical formula. The one most often used is called the *empirical formula*. This gives the number of atoms of each element in the molecule, as H_2O or CO_2. Between adjoining atoms in a molecule there exists an attractive force called a *chemical bond*, which ordinarily prevents the molecule from breaking up into its constituent atoms. The *structural formula* is a means of indicating the bonds as well as the elements that enter into the construction of the compound. These bonds of chemical energy are represented by straight lines connecting the atoms. The two types of formulas can be represented in the case of glucose. This is a simple sugar which is much used in almost all life activities. Its empirical formula is $C_6H_{12}O_6$. Its structural formula is as follows:



This formula, showing the carbon atoms held together by their bonds, and other elements variously attached, makes it evident that this is an organic compound. In introductory botany, empirical formulas are usually sufficient to indicate the chemical processes that must be understood, but occasionally a structural formula is used.

At this point the three great types of organic substance that take part in life activities should be mentioned. Glucose is an extremely simple representative of the *carbohydrates*. These are all made up entirely of carbon, hydrogen, and oxygen. *Fats* are also constructed of these same elements arranged differently and in different proportions. In the case of *proteins*, to these elements there are added some others, especially nitrogen (N), sulfur (S), and phosphorus (P), held together in very intricate patterns.

The Colloidal State. Protoplasm, when active and growing, has about the consistency of fresh white of egg. Such materials as protoplasm, egg white, soap, gelatin, mayonnaise, cream, and glue, to mention only a few that come within everyday experience, belong to a group of substances known as colloids. The name, colloid, was originally coined from two Greek words which mean, literally, gluelike (*kolla*, glue; *eidos*, like). Much remains yet to be discovered about colloids, but a few characteristics which are now well known and which help greatly in an understanding of plant activities should be introduced here.

In the first place, a colloid is not a peculiar compound but is, rather, a system built up of two or more compounds neither of which dissolves readily in the others. Therefore all are associated with each other in a peculiar way. One of these must be very

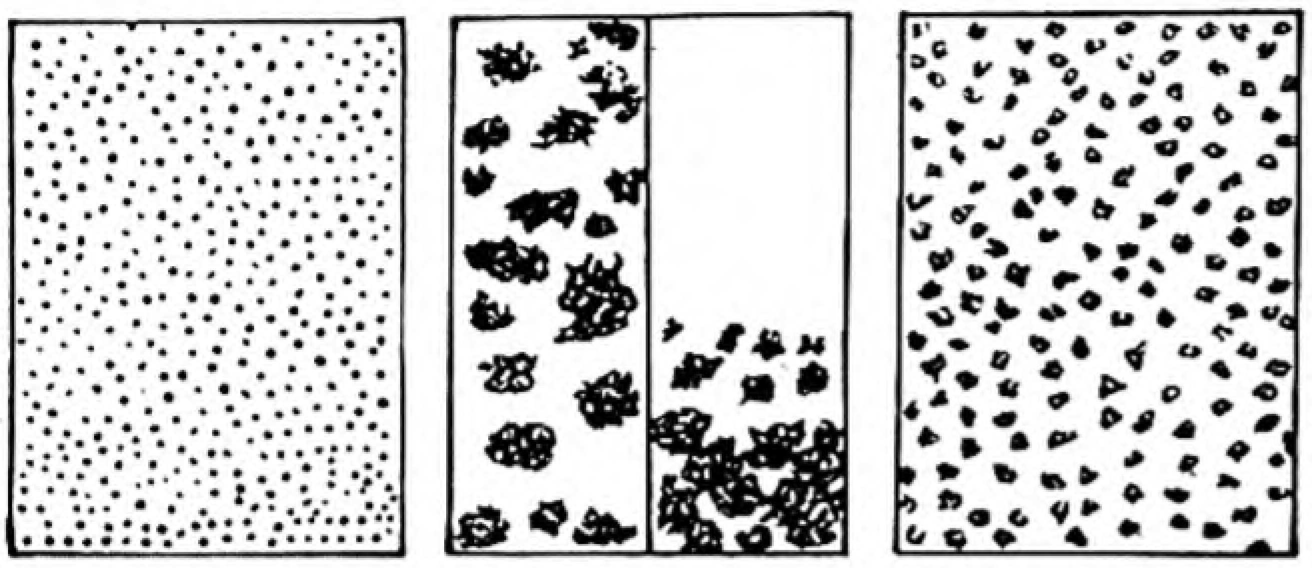


Diagram to illustrate the differences between solutions, suspensions, and colloidal systems. If we could see molecules they would be found to be distributed somewhat as shown. (*Left*) Solution, in which the dots represent the dissolved substance and the clear spaces between, the solvent in which they are distributed. (*Center*) Suspension. Here the molecules occur in such large masses that they settle to the bottom. (*Right*) Colloidal system. The molecules are clumped together in small particles that remain distributed throughout. These are called the disperse phase. The clear part between is called the continuous phase.

finely divided and scattered through the other in such a way that the particles remain dispersed indefinitely. The particles constitute the *disperse phase* of the colloid while the medium in which they are distributed is the *continuous phase*. If the particles are too large to remain distributed in the sustaining medium they form a *suspension* from which they will gradually settle; they are, therefore, not in a colloidal state. On the other hand, if they dissolve, their molecules or even atoms are separated from each other and distributed throughout the medium. This kind of system is called a *solution* and the medium is the *solvent*. Thus the disperse phase of a colloid is composed of particles intermediate in size between those of suspensions and solutions.

The entire plant is constructed of organic substances, including many kinds of carbohydrates, fats, and proteins associated in a great variety of ways. Water usually acts as the continuous phase, and the entire complex is colloidal in nature. Therefore, a complete explanation of many of the activities of plants depends on a knowledge of some of the properties of colloids that are especially important in life and growth processes.

One of the most striking facts of the colloidal state is the extreme amount of surface displayed by the particles of the disperse phase. Someone has calculated that a 1-cm. cube of matter, which would obviously have a surface of 6 sq. cm., would display a surface of from 60 to 6,000 sq. m., depending on the degree of division, if it were changed into the disperse phase of the colloidal state. Since 1 sq. m. is the equivalent of 10,000 sq. cm., these figures mean that the disperse phase of a colloid has an estimated surface ranging from 100,000 to 10 million times as great as the surface of a solid containing the same amount of matter. But almost all the myriad activities of life occur at the surfaces of colloidal particles. Therefore, the great speed with which many chemical and physical reactions must take place during growth, respiration, and other physiologic processes depends in great measure on the colloidal state within the protoplasm.

A second important characteristic of almost all plant colloids is their tendency to take up or *imbibe* water and, in the process, to swell greatly and exert tremendous pressures. Such swelling results from the entrance of water molecules between the molecules of the carbohydrates or proteins, thus forcing them farther apart. In this way the proto-

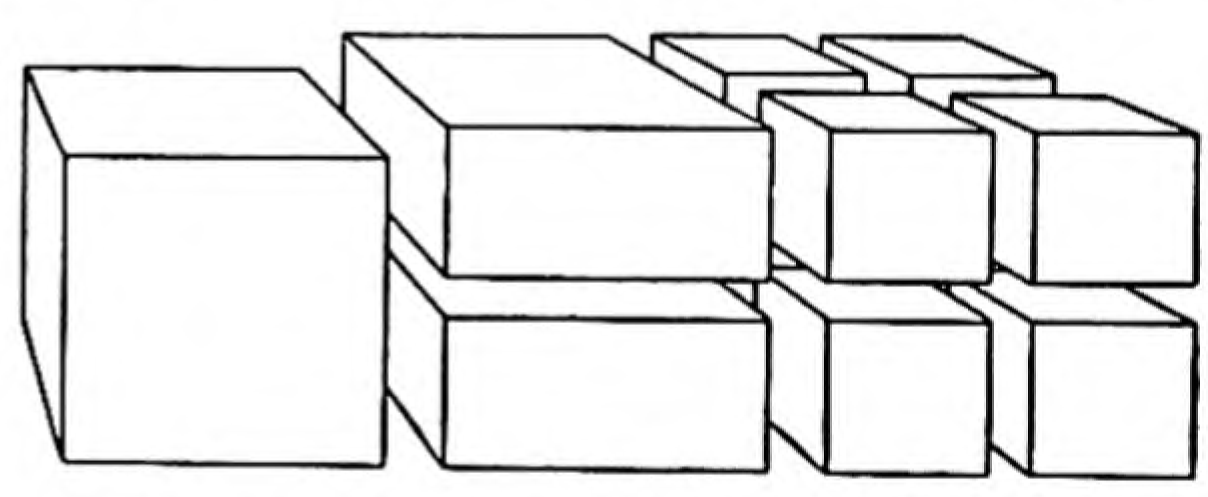


Diagram illustrating that every division of a solid increases the amount of surface. Therefore, the more finely any material is divided the greater the area it displays.

plasm enlarges so much by imbibing water that each cell stretches its walls. Such stretching plays a considerable part in the enlargement of plant cells and even in the shapes they assume. The colloidal state in plants is not limited to protoplasm, for such

nonliving structures as starch grains and cell walls also are colloids which greatly enlarge when they imbibe water. This fact can be illustrated by soaking in water any piece of dry wood, which is almost entirely composed of cell walls. The increased size and the great pressure produced by imbibed water are facts of common observation. As an example, wooden tanks, barrels, and kegs remain watertight as long as they are kept wet, but soon fall apart when the wood becomes dry, reducing the size of the staves and decreasing the pressure on the hoops. Much of the pressure exerted by roots when they lift sidewalks and split rocks is imbibition pressure exerted by both the living protoplasm and the cell walls.

Summary. Botany is a branch of science, that is, of knowledge and discovery, which deals with plants. Plants are living organisms. Life is a phenomenon of protoplasm—a remarkable colloidal mixture. Such life processes as respiration and growth are brought about by chemical reactions in the protoplasm.

SUPPLEMENTARY READINGS

Bonner and Galston, "Principles of Plant Physiology."
Hylander and Stanley, "Plants and Man."
Sears, "Life and Environment."

Chapter 2

LIFE AND ITS ATTRIBUTES

Living things are made of the same stuff as the inanimate objects all around us; and yet, how different is a granite boulder or a clay bank from a tree, or a violet, or an insect! The materials may be much the same in the two cases, but they are organized according to very different patterns.

The following outline is a skeleton which supports the flesh and blood of this chapter on Life and Its Attributes:

Living Things Are Temporary. A patch of horseweed seedlings on a flood plain may have as many as 10,000 young plants per square yard early in the growing season. If a record is kept week by week all summer the numbers are found to decrease rapidly until in the autumn there are seldom more than about 1 per cent remaining. Several causes account for the death of the 99 per cent. Diseases destroy a considerable number; insects eat others; some dry up during summer droughts; and many are the victims of the shade cast by their more sturdy neighbors.

Eventually even the 1 per cent dies after producing the seeds that will carry the plant over winter into the next year. In any event every one of the 10,000 weeds must die at some time during this summer, returning its substance, directly or indirectly, to the soil.

Likewise all other living things, both plants and animals, live for a longer or shorter period of time, may produce offspring, and always eventually return to the nonliving state in which bacteria, molds, and other organisms break their tissues down into simpler substances in the processes of decay. Then, once again, living plants are likely to reassemble these products of decay, to combine them variously into their own structures and to bring them back to play their part in life activities. Thus, many of the common materials of the earth's crust may alternate between the living and

the nonliving states, sometimes being a part of a plant or animal, and at others only the disintegration products of their bodies.

Living Organisms Are Earth-bound. Only a relatively thin layer at its surface, as compared with the diameter of the earth, is commonly inhabited. At a depth of 10 ft. in the soil there are no living things except occasional roots, insects, bacteria, and a few other organisms; above the tree tops, plants and animals become less and less numerous until at a few thousand feet in the air only chance floating pollen grains or other minute plant cells, such as bacteria or the spores of fungi or perhaps infrequent birds are to be found; and in the depths of the ocean living organisms are not common. On this sphere which is about 8,000 miles in diameter, life is limited mostly to a zone not many hundreds of feet thick, and even there the soil, rocks, water, and air greatly outweigh the living organisms.

Living Organisms Are Immeasurably Numerous. Notwithstanding their limitations in space, organisms occur in almost unbelievably extravagant numbers. The mere act of enumerating all the visible living things in a small area in any field or forest—all the individual green plants, fungi, and insects—will prove this statement; and a teaspoonful of rich garden soil often contains millions of such microscopic forms as bacteria, molds, and minute animals.

Organisms Are Extremely Variable. These myriads of living organisms differ from each other almost without limit. About a million distinct kinds, or species, of plants and animals have already been accurately described and have been given standard names, and there is ample reason to believe that the list is far from complete. It also seems probable that no two individuals even of the same species are exactly alike.

Living Things Have Remarkable Similarities. These diverse plants and animals are so organized that, among them, some can thrive in almost every condition to be found from the poles to the equator, from ocean abysses to mountain tops, and from deserts to lakes. Yet with all this variability every individual organism must have certain capacities or it will disappear from the earth. All must be able to acquire food by some means and all must carry on such processes as respiration and growth; and, in addition, members of every species of organisms must be able to produce offspring. And so, while living things are endlessly variable, every one, plant or animal, is fundamentally like every other one. This basic similarity of organisms to each other is a direct result of one single fact: all life activities are carried on by *protoplasm. Protoplasm may be defined as living substance.*

Protoplasm. The name protoplasm (*protos*, first; *plastos*, formed), is applied to the living part of any plant or animal. When the word was first coined about a century ago, so little of its significance was understood that this "primitive slime" was thought to be inert material of little importance. With increasing knowledge, realization gradually came that all life activities are carried on by the protoplasm. We have kept the word but have gradually clothed it with new meaning until the ideas it implies are among the most important to the student of the life sciences.

The activities of this "material basis of life," are varied and intricate in the extreme. Everything that is implied in such processes as growth, reproduction, respiration, and nutrition, to mention only a few, depends on protoplasmic work. It is not surprising then, that protoplasm is so very complex that as yet only the general details of its chemical organization have been discovered. It is true, however, that the chemical elements which enter into its structure are well known, and that it is definitely a colloidal system constructed of particles of many kinds.

The vast majority of these particles are of various kinds of proteins with much smaller amounts of fats and carbohydrates. During active growth of the plant, protoplasm imbibes large quantities of water. In fact, only a very small percentage of the total weight of active protoplasm is of solids, water furnishing most of the remainder of the weight.

To add to the complexity of the system, many substances such as soil minerals, sugars, carbon dioxide, and oxygen are dissolved in the water. But a complete picture of the exact structure of protoplasm is, as yet, impossible to gain for two reasons: Any chemical analysis requires types of treatment

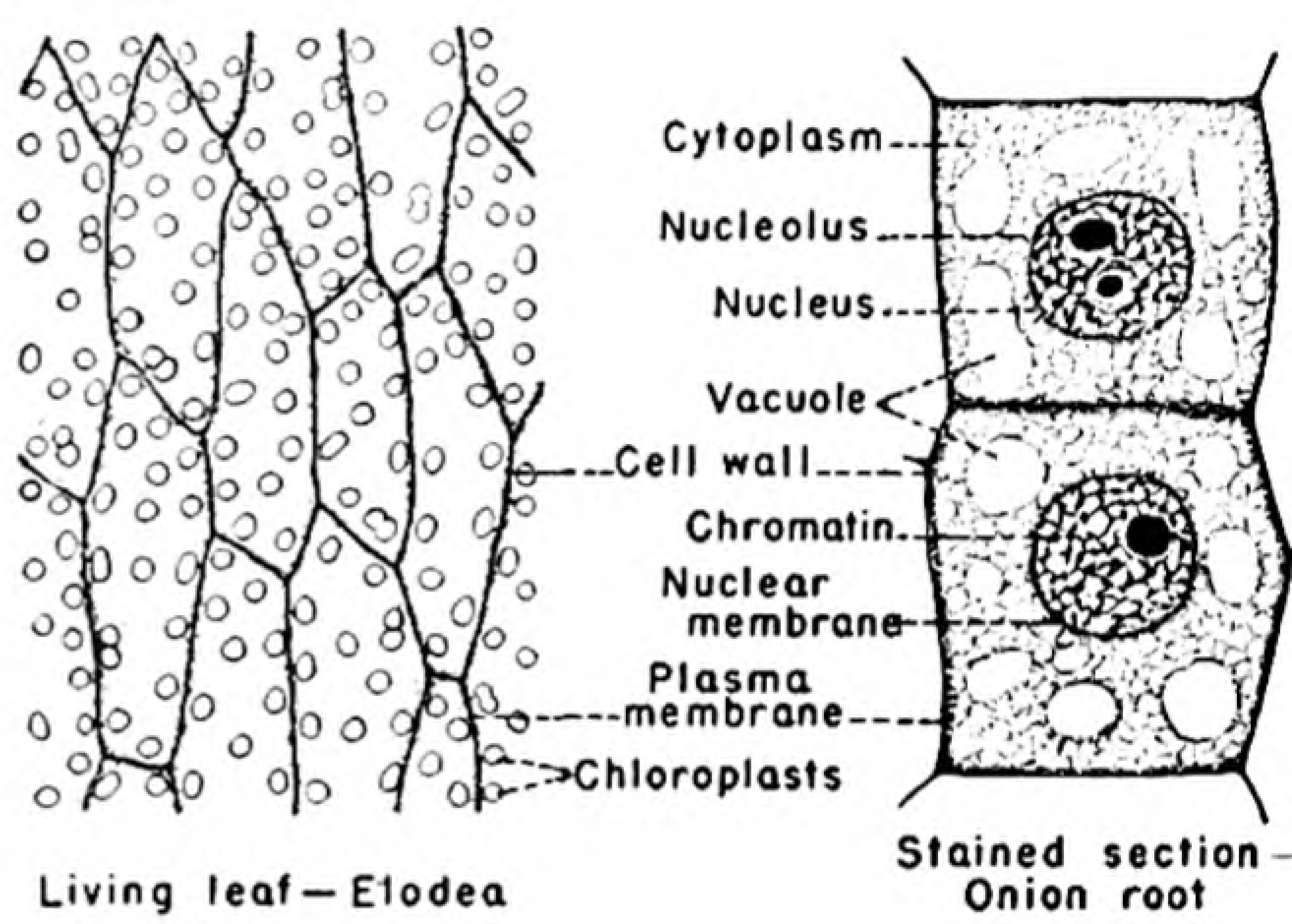
of the substances studied which will cause death, and it is not known just what changes take place in the minute arrangement of parts when death comes. Moreover, the protoplasm of various organisms and even of different tissues of the same body, varies a great deal.

Over a long period of years a search was made to find some special life-substance in protoplasm which is not to be found elsewhere, but all in vain. It seems certain, therefore, that no such material exists. Instead, chemical analysis always shows that protoplasm is composed chiefly of such well-known materials as oxygen, carbon, hydrogen, nitrogen, sulfur, and phosphorus. All of these come ultimately from the nonliving surroundings of living things. The most careful investigations have forced modern biologists to the conclusion that, instead of some peculiar substance which is responsible for life, vital activities are a result of unusual organizations and arrangements of certain of the ordinary materials which constitute the non-living world.

Protoplasm is not usually seen without the aid of the microscope. Of materials that are well known, there is none with so much of the same appearance and consistency as fresh white of egg. This statement does not mean that white of egg is protoplasm, or even that it is chemically exactly similar, but only that to the eye it has much the same appearance. This similarity of appearance comes from the fact that both are colloidal systems made up chiefly of proteins and water.

With these facts in mind one naturally asks how a tree can stand erect when the living parts of it have the consistency of a thin jelly. This question cannot be answered without an understanding of the cell walls of a plant.

The Cell. Protoplasm is usually organized into minute masses called *cells* or *protoplasts* which are almost always too small to be seen without magnification. Their size may be judged from the estimate that it requires from 20 million to 20 billion plant cells to occupy a cubic inch of space. As understood today, *a cell is a bit of protoplasm bounded by a plasma membrane and containing a nucleus or nuclear material.* The part aside from the nucleus is called *cytoplasm.* The nucleus is suspended in the cytoplasm and is surrounded by a very thin nuclear membrane. Inside this membrane there is usually as least one small body called a nucleolus the function of which is not definitely known. In addition there appear to be two rather definite substances, *nuclear sap,* which is more or less liquid in consistency and which occupies the center of the nucleus, and an outer layer, the *nuclear reticulum* (*reticulum,* network) made largely of *chromatin.* Within recent years chromatin has been found to contain materials which transfer hereditary characters from cell to cell and from generation to generation.



Cells.

Other important duties of the nucleus have been discovered by experimenters who have removed the nuclei from living cells by means of a device called a micromanipulator. When the nucleus is thus removed, the cytoplasm lives for only a few days. From such evidence it is believed that there is a definite division of labor between the nucleus and cytoplasm, with the nucleus controlling the constructive growth processes and the cytoplasm having to do with the destructive phases of life activities.

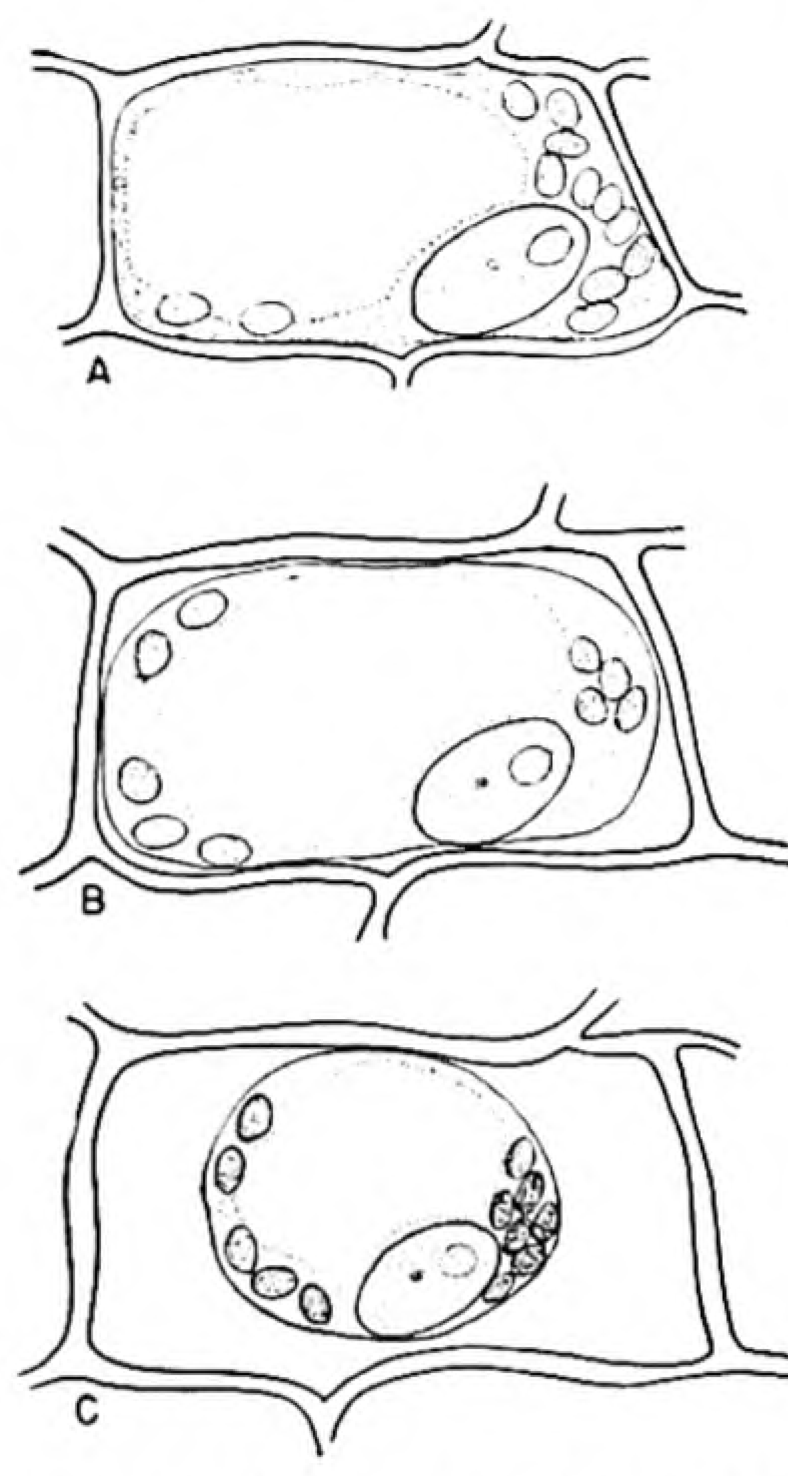
The cytoplasm of plant cells usually exhibits a considerable amount of structure as seen with the microscope. If the tissue has been killed, cut into very thin sections and stained to show details of organization, numerous *vacuoles* can usually be seen. These have the appearance of more or less empty spaces. In the live plant they are filled with *cell sap,* which is often considered to be protoplasm

containing extremely large amounts of water. Many types of substances, such as minerals, sugars, pigments, etc., may be dissolved in the cell sap. As the young cell develops, the small vacuoles scattered through the cytoplasm gradually enlarge and coalesce, eventually forming a large central vacuole surrounded by a thin layer of cytoplasm in which the nucleus usually rests.

The outer surface of the cytoplasm of each cell organizes into a *plasma membrane* which completely encloses all other parts. Whenever the cell is bounded by a wall, as is usual in plants, the plasma membrane lies closely pressed against the wall. So thin and delicate is this membrane that it cannot be seen except in elaborate preparations and with the highest magnifications, but its position can be inferred rather easily by causing the protoplasm to shrink and tear away from the wall. A cell so shrunken is said to be *plasmolyzed*. Plasmolysis can be seen with the microscope if pieces of water plants are mounted in a 5 to 10 per cent solution of table salt. With this kind of preparation it becomes clear that the plasma membrane is a rather firm, but extremely thin enclosing layer over the surface of the cell. The extreme importance of this delicate membrane becomes evident when it is torn or broken, for under these circumstances, it either mends itself or the cell dies. A similar membrane separates the vacuole from the inner surface of the cytoplasm. This is called *tonoplast* or *vacuolar membrane*.

At least a part of the importance of the plasma membrane resides in the fact that it largely controls the kinds and amounts of materials that may enter or leave the cell. By this means it plays an important part in regulating growth and other activities of the protoplasm.

When living plant cells are examined with the microscope, two types of activity within the protoplasm can often be distinguished. With a relatively high magnification and the proper adjustment of light, small particles can often be seen trembling slightly. This motion is not a function of life, but occurs whenever finely divided particles of any kind are suspended in a liquid. This is called *Brownian movement* and is caused by large numbers of rapidly moving molecules of water striking against masses of colloidal particles which are grouped together in large enough bodies to be visible with the microscope. The name, Brownian, refers to Robert Brown, an important pioneer in botanical studies, who demonstrated this motion in



Plasmolysis. (A) A normal cell with plasma membrane pressed firmly against the wall. (B, C) Progressive stages in plasmolysis with more and more of the plasma membrane withdrawn from the walls.

a considerable variety of substances somewhat more than a century ago.

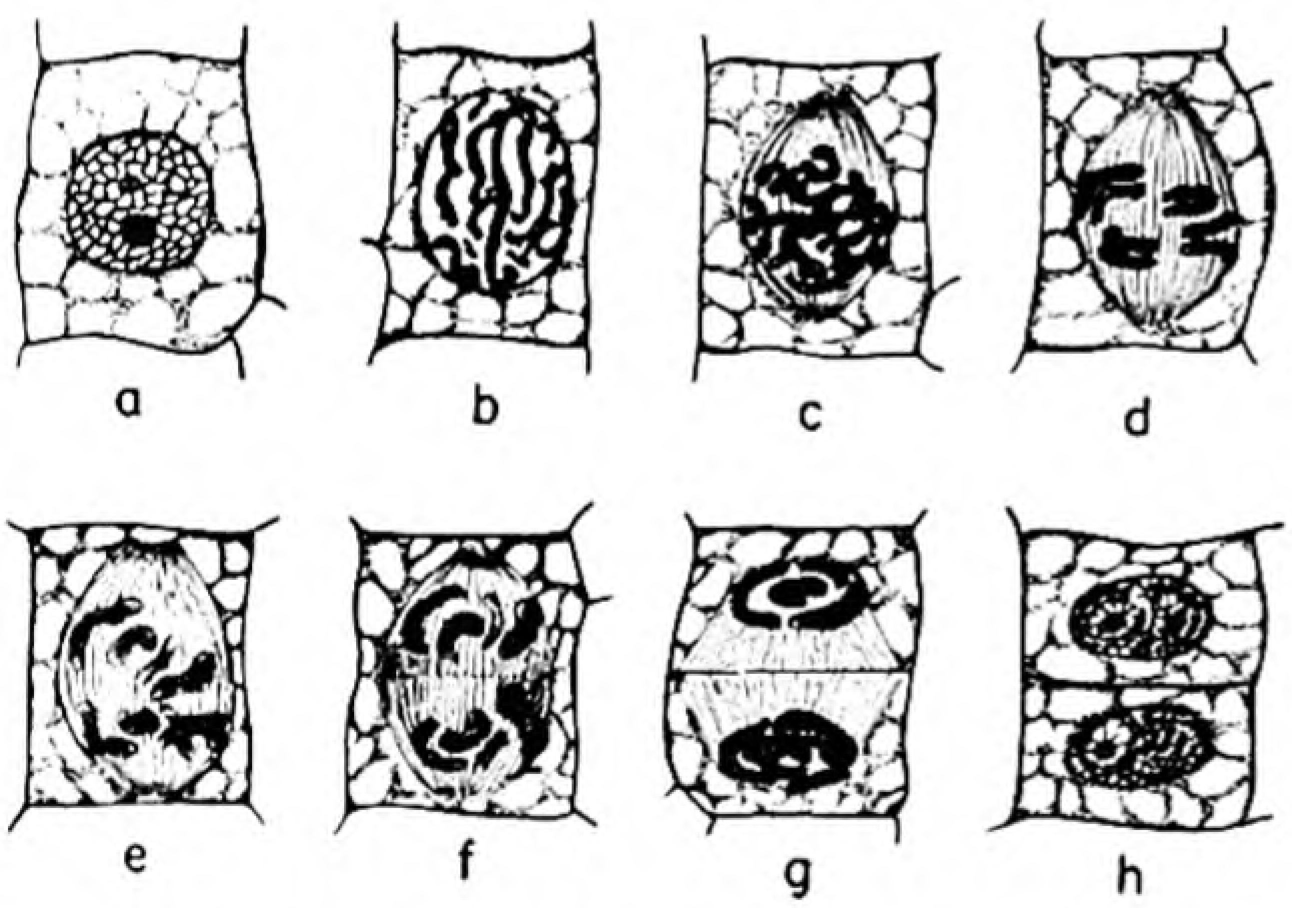
The other type of action in protoplasm, called *cyclosis*, takes the form of migrations of various objects. Not infrequently the nucleus or other clearly defined structures travel the full length or width of the cell within a few minutes. These objects are entirely passive, being carried along by a more or less continuous active streaming of the cytoplasm.

Many plant cells, but by no means all, contain specialized bits of cytoplasm, called *plastids*. Certain of them, the *chloroplasts*, which are green in color, are extremely important in the life of the plant, and will be discussed in some detail in the next chapter. Just now, their presence need only be

recognized. All are closely appressed against the plasma membrane.

Besides the various cytoplasmic structures thus far described, certain nonliving objects which are often encountered in study with the microscope should be mentioned. Among these are starch grains, oil globules, and other foods, as well as certain compounds which appear to have no value to the plant, but which form insoluble crystals in such cells, where they remain indefinitely. These crystals take many forms. Some are slender needles that occur in bundles, others are rectangular, and still others form aggregates with corners pointing in all directions.

Cell Division. Many cells in a plant body have the ability to reproduce themselves. We are not fully prepared at this point to examine, in detail, the way in which this process is carried on, but in order to be able to comprehend succeeding steps it will be necessary to have in mind a few of the facts.



Mitosis. Somewhat simplified drawings of steps in mitosis. (a) Chromatin network of nucleus that has not begun to divide. (b, c) Formation of the chromosomes and spindle fibers. (d) Splitting of the chromosomes. (e) Migration of daughter chromosomes. (f, g) Formation of cell walls and division of the mother cell into two daughter cells. (h) Organization of the daughter nuclei.

To illustrate: A mature seed plant which is composed of almost innumerable cells, was, at first, a single fertilized egg in the developing seed. This cell divided into two similar ones, these two into four, these into eight, and so and on, until there was produced a mass of several hundred. As time went on and the numbers increased to the thousands, some lost the power of division, while a considerable number continued to divide indefinitely. From these almost endless divisions, each of which made two cells from one, came this plant constructed of its myriad bits of protoplasm, most of which are surrounded by more or less firm walls.

This process of cell division is an extremely complicated activity, but for the present only a few of the more obvious actions need be outlined, leaving for a later discussion (p. 154) some of the finer details and their meaning.

In a dividing cell the chromatin network within the nucleus changes into rod-shaped portions, the *chromosomes*, each of which splits lengthwise forming two daughter chromosomes, which separate from each other and move to opposite ends or sides of the cell. Here the two sets of daughter chromosomes become organized into two new nuclei similar to the one from which they were derived. This complete series of changes is commonly called *mitosis*. At about the time when these mitotic activities come to an end, a wall forms between the two young nuclei, dividing the cytoplasm and making two new cells. A few hours later each of these may be full-grown and ready to repeat this complicated process. In this way the untold millions of cells which make up the body of a large plant come into existence.

Mitosis plays another important part as well. It is the means by which every cell receives its inheritance, a fact which will become apparent in following paragraphs. This fact must be interpreted, however, in the light of another, as indicated in the outline below:

Living things are under a two-fold set of controls:

(1) Controls exerted by heredity—that is, the genes.

(2) Controls exerted by environment.

Genes. We have seen (p. 1) that the individual plants of a modern field of high grade corn are remarkably uniform as compared with those of a similar field a few years ago. We have also seen that this change has come about through the work of expert plant breeders who have been able to unite

desirable hereditary traits in developing these new, improved strains. While field corn is used as an example, it is known that the same principles apply to plants and animals of all kinds. Whatever the organisms, inherited characteristics result from the presence in the cells of certain controls of heredity. These are commonly called *genes*.

Each cell has thousands of genes and, ordinarily, every body cell of an individual plant or animal has the same set as all the rest that compose that body. But two individuals are seldom, if ever, exactly alike because of differences in gene combinations. For this reason one stalk of common field corn may be dwarf while another is tall when the two are growing together under the same conditions; one may have small grains while another has large ones; some grains may be white while others will be red, yellow, blue, or purple; and one plant may be sturdy and healthy while another cannot even maintain life until it reaches maturity.

The breeder of fine corn, then, is successful only when he finds ways to eliminate unsatisfactory gene combinations and to unite the most desirable ones. The methods used cannot be discussed here but will be considered in some detail in Chapter 10. It should be understood, however, that the lack of uniformity that was described in the corn raised in earlier years resulted from the fact that, at that time, no one had discovered a way to separate the good from the poor gene combinations in even the best of the strains of field corn of the day. Therefore, the various kinds grew together, with the low grade individuals occupying the space that might have been held by more productive ones.

Differences in genes and their groupings produce not only such minor variations as were described in corn, but the greater ones which separate the species from each other. As an example, corn is unlike oak trees, algae, or ferns because it does not have a combination of hereditary determiners similar to any of these.

Genes and Mitosis. In an earliar paragraph the statement was made that mitosis is the means by which every body cell receives its inheritance. The statement was also made that the genes are the determiners of heredity. We are now in position to relate these two facts, for the discovery has been made that each chromosome carries a large number of genes arranged in a row throughout its length, like beads on a string. In the process of mitosis, by which a nucleus gives rise to two new ones, each

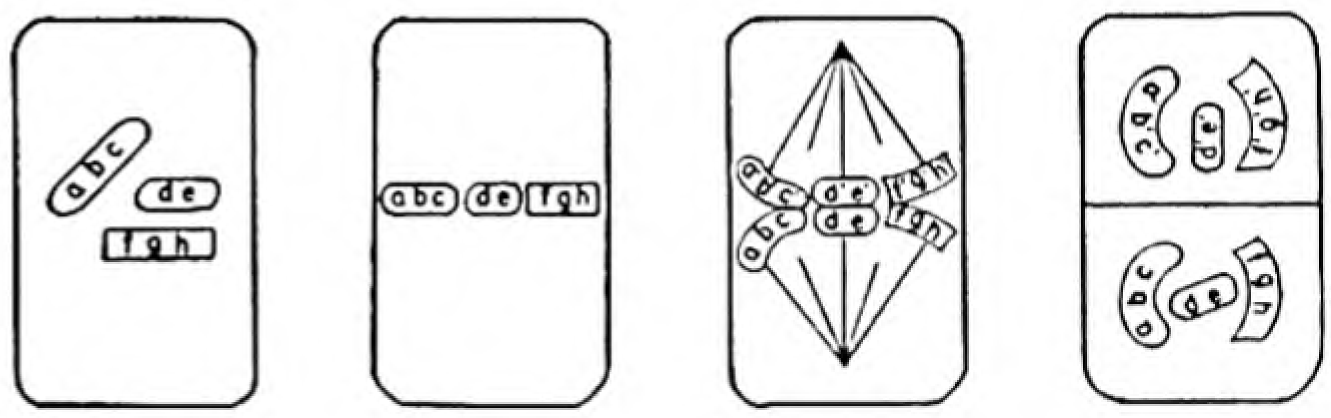


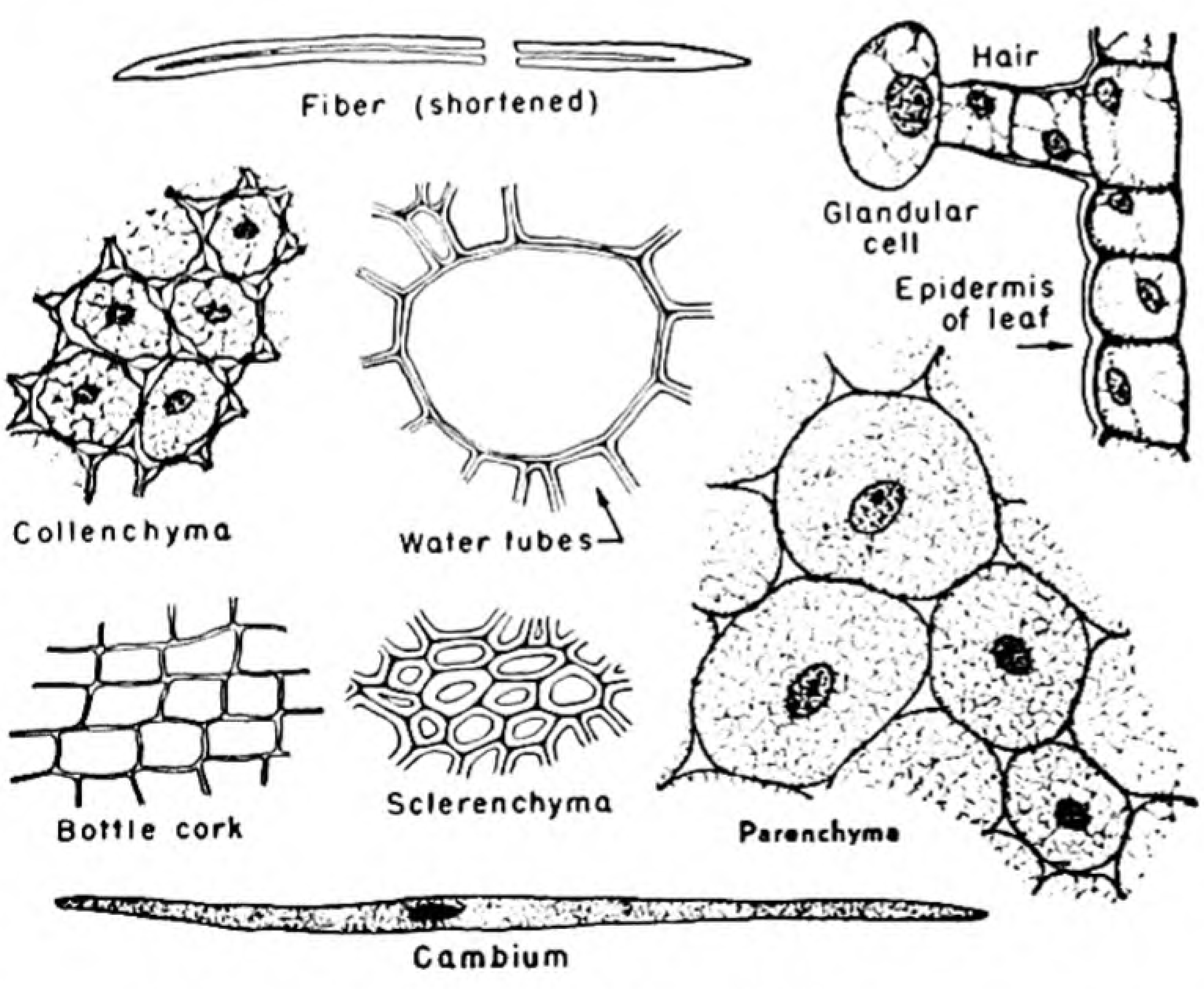
Diagram of dividing cell with three chromosomes, each of which carries genes represented by letters. Notice that each of the two daughter cells has the same set of chromosomes and genes as the mother cell.

chromosome splits lengthwise, forming two daughter chromosomes. In some way, as yet unknown, each of these carries the same quota of genes as the mother chromosome from which it arose. This process is repeated as mitotic division follows mitotic division in all the dividing cells which eventually form the developing organism. Therefore, every cell of the entire plant body may be expected to carry the same quota of genes as every other one, in this way controlling the hereditary characteristics of the entire individual.

The Action of Environment. One other factor enters in to complicate the situation, however, for with a given gene combination, the surroundings or environment set the limits for the effects of the genes. Take, for example, a plant whose heredity would cause it to grow tall under ideal conditions. If it chances to be in poor soil or has insufficient water it is dwarfed by its environment. Or again, a red-flowered plant may, if grown in the shade, have pink flowers. In each of these instances the gene complex was right to produce a fuller expression of the characteristic in question, but some phase of the environment prevented its complete development. In like manner all protoplasm is subjected to two influences. The one arises from within in the form of the combined activities of its genes, and the other comes from the environment which to a greater or lesser extent controls the effectiveness of these genes.

The results are, therefore, the products of the hereditary constitution of the organism and the effects of the environment. Either of these may be faulty, making an imperfect product. Environment may be compared to a machinist and the genes to the metal with which he works. If he is an unsatisfactory workman, even the best of steel in his hands can become only an ineffective machine; if he is skillful and the metal is faulty, the product still is substandard; but the best results are obtained when both the workman and his metals are of high quality.

Differentiation. New cells, as stated above, are formed by mitotic divisions. After they organize, however, they seldom remain unchanged. Instead, they grow in size and many of them take on new shapes. As a result, even casual examination of plant structures with the microscope reveals many kinds. Some are relatively large and others small, some have thick walls and others thin, some are long and narrow while others are short and wide, and various combinations of sizes of cells and thickness of walls occur.



Cells and cell walls of different kinds of tissues.

Those cells of a given type tend to be grouped together into structures called *tissues*, each of which has at least one rather definite function. For example, certain groups become long, hollow tubes that transport water through the plant; others develop extremely thick walls, become greatly lengthened, and afford mechanical strength; others organize rich protoplasm that secretes various substances; while still others protect the surface of the plant from drying and external injury. These are sometimes classified according to function as *conductive*, *mechanical*, *glandular*, and *protective* tissues; and ancestral to all the others are the *formative* tissues.

A thorough examination of an entire plant shows that mitosis is largely limited to certain parts in which growth is a primary function. These groups of cells are called *meristems*, that is to say, *a meristem is a formative tissue*. Such a formative tissue occurs at the tip or apex of every growing root or shoot. Because of its position at the apex, it is called an *apical meristem* (see illustration on p. 18). Apical meristems are responsible in several ways for growth in length of both stems and roots. In fact, all the older parts of these organs are directly or indirectly their descendants.

A careful examination shows the various cells of apical meristems to be remarkably similar to one another. All are nearly cubical in form and have thin walls and abundant protoplasm. If the older parts of such a plant are examined, it becomes evident that during the processes of growth and maturing, certain groups of cells change gradually into specialized tissues that have become different from each other and from the cells of the apical meristem. This process of change is called *differentiation*.

Cell Walls. Cells of plants are usually, but not always, surrounded by walls. These form between the two cells at the end of each mitotic division and soon become more or less rigid and fixed in shape. They are products of the activities of the protoplasm but are not, themselves, alive. These walls constitute a sort of framework which, to a considerable degree, maintains the shape of the plant body. While the jellylike protoplasm is not firm enough to hold itself upright in the form of a complicated plant, the walls that form around the

cells keep each microscopic bit of living substance in position, thus maintaining the shape of the entire mass. Even after the death of a tree or other woody plant, the walls remain in their original places and the greater part of the plant holds its form although the protoplasm is gone. The shape assumed in the first place depends on the activity of growing protoplasm, but when the walls are fully developed around the cells, further change of form does not take place.

The chemical structure of cell walls varies considerably, but the basic substance, whatever materials may be added, is usually *cellulose*, a carbohydrate rather closely related, chemically, to starch. Walls of pitch cells and cotton fibers are almost pure cellulose. During the development of wood, *lignin*, a carbohydrate derivative is added to the original cellulose. The tensile strength of wooden timbers, which is about the same as that of wrought iron, is due entirely to the chemical organization of the cellulose. The lignin is an amorphous waxlike substance which occupies infinitesimal spaces among the cellulose fibers. In like manner, the walls of cork cells become impregnated with a waterproof material called *suberin*.

Changing Knowledge of Cells. Long before the invention of the microscope a few thinkers suspected that living things are made up of bits of material too small to be seen. Such conjectures were only hypotheses acknowledged to be beyond proof or disproof by the means then at hand. Actual certainty came only with the development of the microscope. This instrument did not appear as a single invention but rather as the result of patient experimentation by many men scattered throughout western Europe. A remarkable network of circumstances, some of which contributed only incidentally, brought forth the earliest microscopes. First in this series of events came the printing press and the production of books. The advent of the printed page stimulated large numbers to learn to read. Then there arose a strong demand for spectacles to correct faulty vision. As a consequence, lens grinding became a profession. About 1590 two expert lens makers, Hans and Zacharias Janssen in Holland tried the experiment of fitting a convex lens into each end of a six-foot tube, pointing one end at a small object and peering through the other. This seems to have been the first *compound microscope*. In contrast with the *simple microscope*, which is a single piece of glass such as a reading glass, the compound microscope is an instrument in which one lens, the *ocular*, enlarges the already magnified image of another, the *objective*. Later models produced by these two men were much smaller and therefore less cumbersome than their first model. But the best they were able to make are said to have magnified not more than nine diameters. This magnification is somewhat less than that of the present-day tripod lens in common use for the examination of fairly large objects but by no means useful for more exacting work.

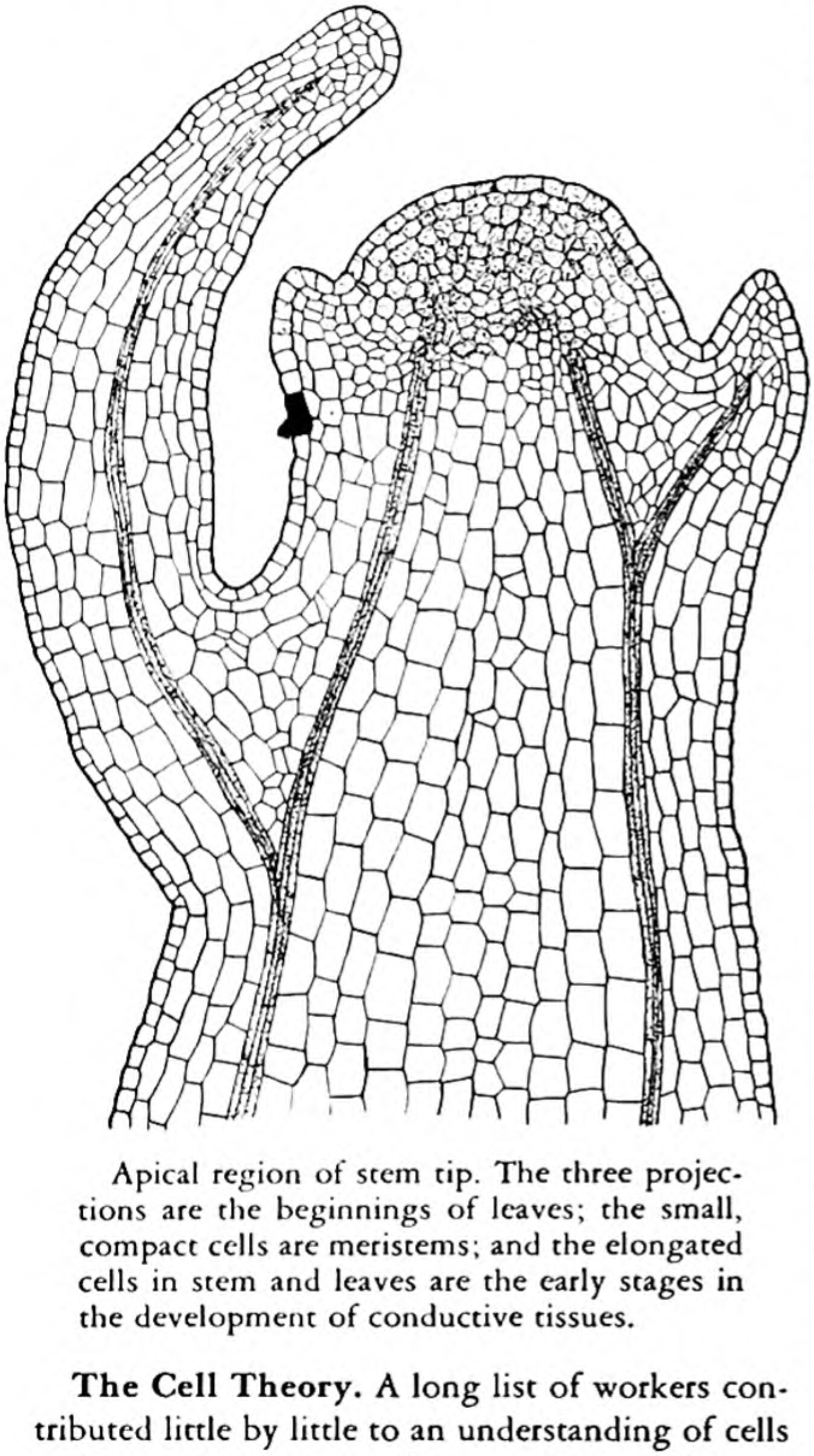
Following the Janssens' invention, the next 150 years saw a veritable ferment of activity in the development and use of the microscope. In 1609 Galileo, the pioneer Italian astronomer, rearranged the lenses of a telescope and made a microscope with which to examine many objects that met his fancy. He added little to the knowledge of any phase of biology, but improved the mechanics of the microscope in a large number of ways. Some of these improvements were adopted by other experimenters, and added greatly to their success. And so the fame of the lenses spread.

In 1665 Robert Hooke in England published a large book, "Micrographia," in which he dealt with all sorts of small objects he had examined with a crude compound microscope. Among other things he included the first known account of the internal structure of plants, illustrated with numerous original drawings.

The illustrations on pp. 19 and 20 are photographs from "Micrographia" in which Hooke described his method of work and proposed the use of the word, *cells*, as a name for the microscopic compartments he had discovered.

The term, cell, has been used for over two and one-half centuries since this first publication by Hooke, but its meaning has gradually changed with increasing knowledge. Hooke had no idea of protoplasm as the fundamental substance of plant structure. Rather, he observed only nonliving cell walls and understood little of their meaning.

Returning to the modern definition of cells given earlier in this chapter (p. 12), the student should definitely determine the difference between the original meaning as used by Hooke and the present-day interpretation of the word.



Apical region of stem tip. The three projections are the beginnings of leaves; the small, compact cells are meristems; and the elongated cells in stem and leaves are the early stages in the development of conductive tissues.

The Cell Theory. A long list of workers contributed little by little to an understanding of cells and protoplasm. Many of these earlier investigators with the microscope became familiar with the fact that plants and animals are constructed of cells that are essentially alike. Most of these men were aware that the cell walls of plants are filled with some substance, but were very uncertain as to its structure or significance. As early as 1824 Dutrochet in France reached the conclusion that "the cell is the fundamental element of organization." In 1831 Robert Brown in England reported that he had found the *nucleus* in many kinds of cells and had given it its name. And in 1846 Mohl in Germany named *protoplasm*. During this period of intense investigation, a rapidly expanding group of workers was developing throughout western Europe. Each was making discoveries and interpretations and thereby stimulating the others.

In 1838 and 1839 two young German scientists, Schleiden, a botanist and Schwann, a zoologist, summarized the work of their predecessors in a way that clarified much of the thinking concerning cells from that day to this. We still refer to this summary as the *cell theory*. Subsequent research has shown their basic idea to be fundamentally correct and therefore no longer only a theory. This concept expressed in modern terms amounts to this:

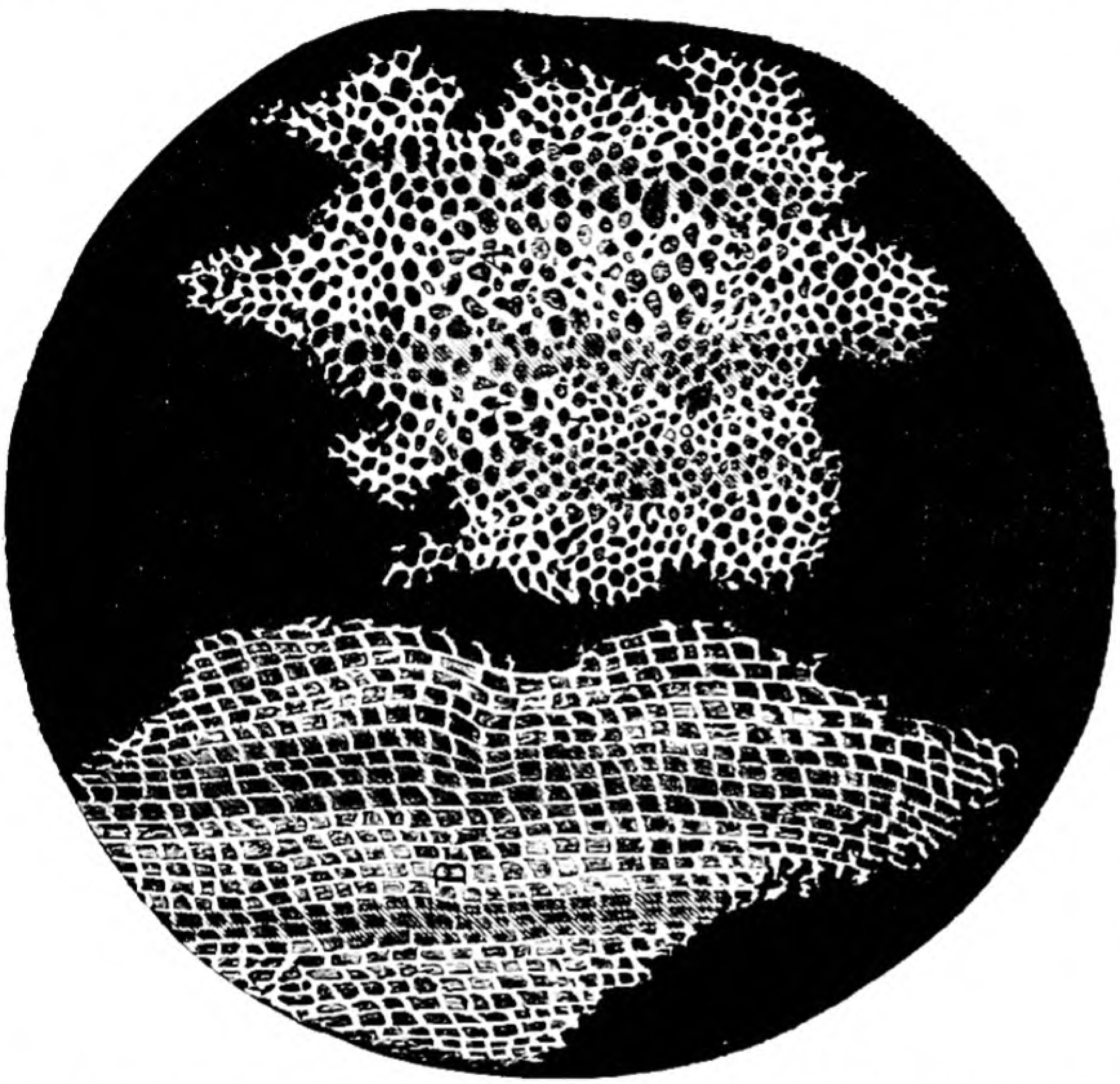
1. The cell is the fundamental unit of plant or animal organization.
2. All life processes of whatever nature are carried on by individual cells rather than by the organism as a whole.
3. Cells originate in no other way than by division of other cells.

This condensed outline fairly well expresses the greatest degree of advancement in understanding the minute structure and activity of plants that had been achieved up to about 1839.

The modern compound microscope, which is in continuous use throughout the civilized world, uses the principle discovered by the Janssens, but with countless refinements in both construction and manipulation. Lenses, mountings, and adjustments are almost unbelievably superior to even the finest instruments of only a century ago, and improvements are being made continually. The best of the compound microscopes yield magnifications up to about 2,000 diameters. Remarkable new departures are now being developed in the phase microscope and in combinations of X ray, the electron microscope, and photography. These are supplementing the older equipment. With magnifications exceeding 2,000,000 diameters details are becoming visible that could be only

suspected before. By combining all the means at hand the investigator is delving deeper and deeper into the unknown. What the new discoveries will be only the future can tell.

The Origin of Life. From ancient times until about three centuries ago, the generally accepted idea was that living things often arise from mud, decaying materials, or other nonliving substances under the action of the sun or some other force of nature. This idea is termed the "spontaneous generation" of life. Almost all of the ancient literatures are filled with references to such phenomena. Spontaneous generation was usually taken for granted without any apparent thought that proof was needed. The mud of the Nile was supposed to produce frogs, flies, and many other highly organized animals, and decaying flesh was thought to give rise to bees and flies. Even after careful experiments had been made by Redi, an Italian investigator, a little less than three centuries ago, and by a series of others down through the years, many scientists for a long time failed to understand the fact that organisms are derived from parents and not from nonliving things. Even van Helmont, whose fine pioneer work on photosynthesis is described in Chapter 3, gave a recipe for producing mice spontaneously from a mixture of old rags and other things. As late as 1819 a writer stated that "algae, lichens, and mosses may develop without seed from decomposing water." It remained for Pasteur, in 1860, to prove finally that even the lowliest of plants and animals come from previously existing creatures of their kind. Even to the present time there are many nonscientific people who are certain that spontaneous generation frequently occurs. Examples of such erroneous beliefs are the ideas that horse hairs in water may become snakes; that earthworms form spontaneously and fall with rain; and other equally impossible notions.


Cork cells. The first known drawing of cell walls. Published by Robert Hooke in 1665.

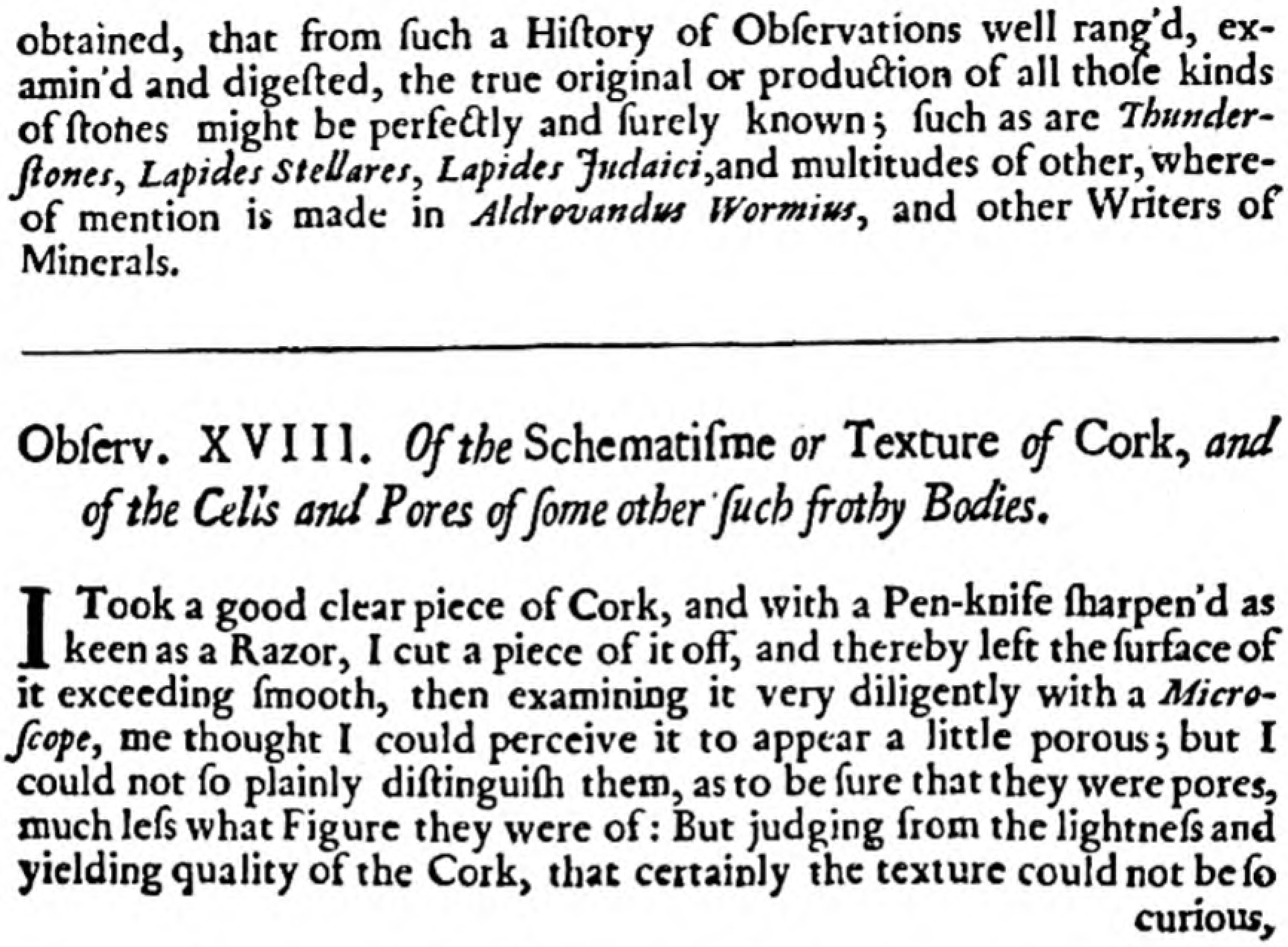
There is abundant evidence that complex organisms do not arise without ancestors, but there is little proof of the time, place, and form in which life first appeared on earth. It is known, however, that life has been here for hundreds of millions of years, because geologists have been able to determine with a fair degree of accuracy, the ages of rocks in which are imbedded records and often even the actual structures of plants and animals. Some of these fossil remains are old almost beyond the ability of the imagination to conceive. Estimates based on careful study by geologists place the origin of life on earth at a time more than a billion years ago.

Summary. Life is known to have been on earth for many millions of years, but the conditions and the place or places where it first came into existence remain shrouded in mystery. So far as is known, life

never occurs except in protoplasm, an extremely complicated colloidal system constructed of particles of many kinds. During active growth it imbibes great quantities of water, and to add to the complexity of the system, many substances such as soil materials, sugars, carbon dioxide, and oxygen are dissolved in the water.

Living things are set off from nonliving, not by being constructed from peculiar substances, but because of the unique organization which permits life processes to go on effectively.

Protoplasm is usually organized into small structures, the cells. Each of these is, characteristically, made up of a nucleus surrounded by cytoplasm, which, in turn, is covered by a specialized layer, the plasma membrane. Usually vacuoles occur, filled with cell sap. Sometimes nonliving inclusions such as starch grains and mineral crystals occur. In many cells there are living plastids. The protoplasm of a single cell is an almost unbelievably complex organization of colloidal particles, masses, and membranes, the disperse phase of which varies greatly between the parts.



obtained, that from ſuch a Hiſtory of Obſervations well rang'd, examin'd and digeſted, the true original or production of all thoſe kinds of ſtones might be perfectly and ſurely known; ſuch as are *Thunder-ſtones*, *Lapides Stellares*, *Lapides Judaici*, and multitudes of other, whereof mention is made in *Aldrovandus Wormius*, and other Writers of Minerals.

Obſerv. XVIII. *Of the* Schematiſme *or* Texture *of* Cork, *and of the Cell's and Pores of ſome other ſuch frothy Bodies.*

I Took a good clear piece of Cork, and with a Pen-knife ſharpen'd as keen as a Razor, I cut a piece of it off, and thereby left the ſurface of it exceeding ſmooth, then examining it very diligently with a *Microſcope*, me thought I could perceive it to appear a little porous; but I could not ſo plainly diſtinguiſh them, as to be ſure that they were pores, much leſs what Figure they were of: But judging from the lightneſs and yielding quality of the Cork, that certainly the texture could not be ſo curious,

Photograph of a page from "Micrographia" by Robert Hooke, showing where he proposed the name "cell" for the plant structure.

During the growth of a plant, cells increase in number by a complicated process called mitosis in which the nucleus divides, and one cell becomes two. As the newly formed cells mature they change shape, develop various types of walls, and organize into tissues. In other words, they differentiate.

Genes, or determiners of heredity, are transferred from mother cell to daughter cells by the process of mitosis. The combinations of genes determine the hereditary potentialities of the plant but the effectiveness of these potentialities is limited by environment.

SUPPLEMENTARY READINGS

Guilliermond, "The Cytoplasm of the Plant Cell."
Mayer, "The Cell Theory."
Nordenskiold, "The History of Biology."

Chapter 3

LEAVES, THE PRODUCERS OF FOODS

The verdure of a summer landscape—of forest, of prairie, of mountains—is so beautiful that it inspires poets and painters with many themes, and often gives unexpressed thrills to the rest of us. But few of us realize that we could not remain alive without this selfsame greenness. This chapter deals directly or indirectly with the food we eat, the clothes we wear, the fuels we burn, and the air we breathe. The following outline should help to keep in order the numerous facts presented here.

Grasshoppers eat plants, many birds nourish themselves by devouring grasshoppers, and such predators as cats, foxes, and wolves feed on the birds. By some such series of steps, food passes from one organism to another, in each case furnishing the body-building materials and the energy by which life processes are carried on. Food may be defined as *any substance that can become a part of the*

body of a living organism and can release the energy used in life processes.

Whenever any food chain is traced back to its source, it ultimately ends with green plants. These plants produce simple sugars by a process which has been named *photosynthesis* (*photos*, light; *synthesis*, placing together). The significance of the word will become obvious in the next paragraph.

PHOTOSYNTHESIS

Present-day understanding of photosynthesis, the primary food-making process, may be summarized in the following definition: *Photosynthesis is the manufacture of simple sugars and oxygen from carbon dioxide and water in the chloroplasts* (the green color bodies) *in the light.* Stated in chemical terms and thinking of glucose as the sugar formed, we have the following equation:

$$\underset{\text{Carbon dioxide}}{6CO_2} + \underset{\text{Water}}{6H_2O} \rightarrow \underset{\text{Glucose}}{C_6H_{12}O_6} + \underset{\text{Oxygen}}{6O_2}$$

This equation means that six molecules of carbon dioxide are combined with six molecules of water, forming one molecule of glucose and six molecules of oxygen. The oxygen commonly escapes into the air. This chemical reaction takes place wherever and whenever suitable amounts of water and carbon dioxide come together in chloroplasts under the influence of light and at a proper temperature.

Light and Photosynthesis. Numerous carefully controlled experiments have given ample proof that the process of photosynthesis ceases at once when darkness comes and is resumed quickly with the return of a proper light intensity. Obviously, then, light is essential to the process.

Light is one of the best-known forms of energy, others being heat, motion, and that which takes part in chemical reactions. Energy may be *potential* (inactive or stored) or *kinetic* (active) and, under suitable conditions, either of these forms can be changed into any of the others. As examples, gasoline, which has a great deal of the potential form of energy, can be caused to explode, liberating kinetic energy in the forms of heat, light, and motion; or a charged electric battery may change its potential energy into kinetic form as heat, light, or motion when it is properly connected with suitable appliances. For present purposes it is necessary

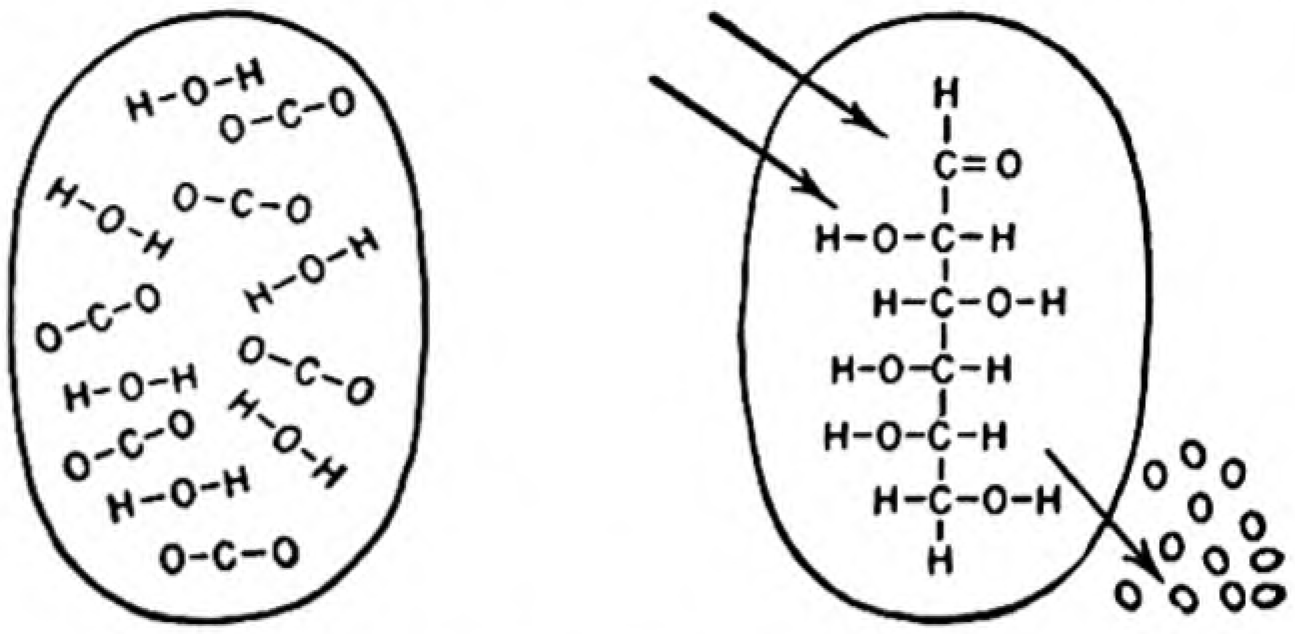


Diagram of chloroplast containing six molecules of carbon dioxide (O–C–O) and six of water (H–O–H). (*Left*) Before photosynthesis has occurred. (*Right*) After light, represented by two arrows, has entered. A molecule of glucose has been formed and the excess oxygen is escaping.

only to know that energy can take many forms and that any of these can be changed into any of the others.

Light, a Form of Energy. The light which comes from the sun seems to be colorless. It is ordinarily spoken of as "white light," and it has the appearance of being simple. But a common experiment readily shows that sunlight is complex. If a beam of it is passed through a glass prism and allowed to fall on a suitable screen, it is changed into a series of colors like those seen in a rainbow. By careful examination, it is possible to distinguish more or less clearly a series ranging from deep red, through orange, yellow, green, blue, and indigo, to violet. These are known as the colors of the *spectrum*.

The physicist recognizes these various forms of light as manifestations of radiant energy. This energy behaves as if it were in the form of waves, pulsations, or vibrations. He has been able to measure the lengths of these waves and has found them to be relatively short. The longest the human eye can perceive give the sensation of red; they are about 28-millionths of an inch long. The shortest visible waves, which are at the violet end of the spectrum, are about half as long. Both much longer and much shorter waves of radiant energy are

known, but the human eye does not perceive them. Beyond the red are longer ones known as *infrared* (*infra*, below), which grade over into even longer *heat rays*, and the still longer ones used in radio. At the other extreme are those shorter than violet. Just shorter are the *ultraviolet*, which are invisible to the human eye but which cause sunburn and tanning of the skin. These are followed by the still shorter and more penetrating *x-rays* and finally by the shortest known *cosmic rays*, some of which have wave lengths not more than a 10-millionth as long as violet light.

Within this vast range the human eye is blind to all but a minute group of rays, violet to red, which make up a tiny island in the vast ocean of energy pulsations which surrounds us. Strangely enough, in photosynthesis the plant appears to use only the light visible to the human eye, and only a part of that. This is another way of saying that photosynthesis does not occur in the dark, the dark representing all parts of the radiant energy to which human eyes are not sensitive.

The Light Used in Photosynthesis. About three-quarters of a century ago the German botanist, Sachs, devised an experiment to test the effects of different colors of light in photosynthesis. Certain green plants were placed in red light and others of the same kind were placed in blue. After sufficient time had been allowed for photosynthesis to take place, tests showed much more starch in the plants that had been in the red than in those that had been in the blue light.

Later experiments carried on by another German botanist, Engelmann, added striking confirmation to Sachs' conclusions. Engelmann arranged a prism in such a way as to cast a complete spectrum in the field of his microscope. He mounted some very simple plants (green algae) in water containing a culture of freely swimming bacteria which tend to move toward supplies of free oxygen. On single cells or threads of the algae he cast a spectrum in such a way that different colors fell on different parts of the plant. As stated above, a green plant gives off oxygen as a by-product of photosynthesis. The bacteria would, therefore, be expected to congregate in the regions where photosynthesis was taking place and where oxygen, therefore, was abundant. The experiments showed them in greatest numbers in the orange-red light and in somewhat smaller numbers in the blue-violet region, while relatively few remained in the yellow-green

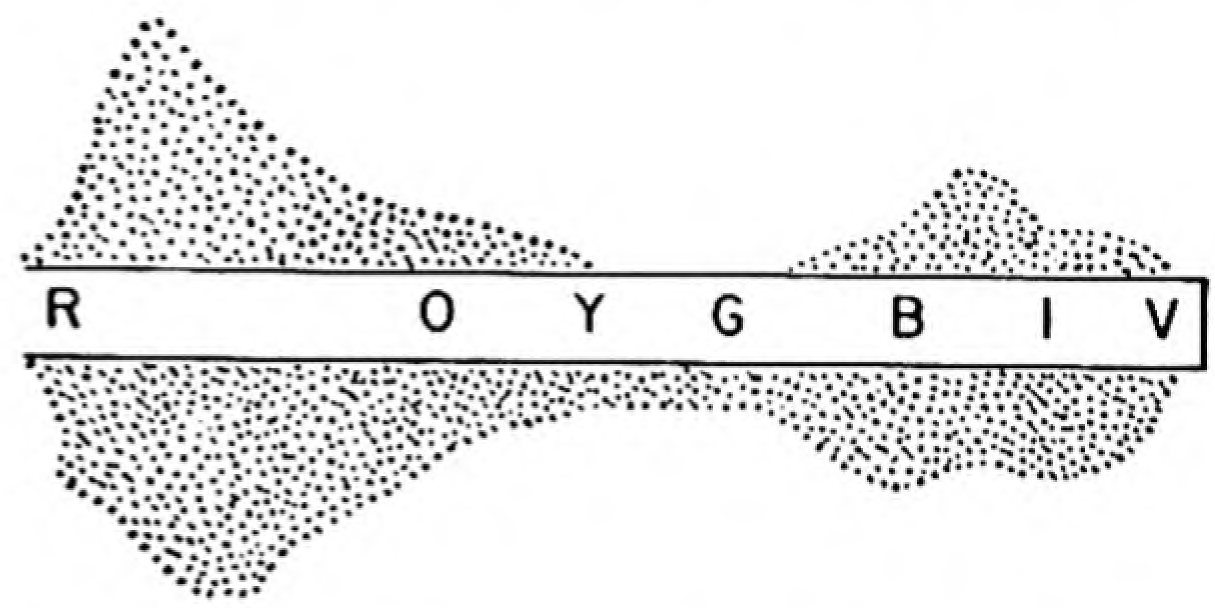


Diagram of Engelmann's experiment, showing arrangement of swimming bacteria around plant cells in which photosynthesis was taking place. (R to V) Positions of colors of spectrum from red to violet. (Adapted from Palladin after Engelmann.)

part. What conclusions could properly be drawn from these observations?

It would seem that a part of the explanation of these facts may be gained by an understanding of some of the peculiarities of chlorophyll. If all the pigments from the chloroplasts of a plant are dissolved with alcohol and a vessel of the solution is placed in the path of a beam of light before it enters a prism, a normal spectrum is not obtained. Instead, there is a rather wide dark band where the red-orange would be expected and another in the region of blue-violet. This means that the light responsible for these parts of the spectrum has been absorbed by the solution of chlorophyll and other pigments from the chloroplasts.

Under natural conditions the light used in photosynthesis comes directly from the sun. It should be understood, however, that any light of proper intensity and of suitable wave length is entirely effective. The following experiment will illustrate: A basement room without windows was fitted out with ordinary greenhouse benches and soil. Electric lights with large reflectors were hung a short distance above the soil level and seeds of numerous kinds were planted. With no light from any other source than these electric bulbs various crop plants, garden vegetables, and weeds were grown to

maturity and some of them produced healthy seeds.

Chlorophyll and Photosynthesis. Certain observations made in connection with these experiments can now be brought together to give additional suggestions as to the part which chlorophyll plays in photosynthesis. It has been proved that the process will take place in any suitable light without regard to its source. The experiments of Sachs and Engelmann have shown that red light is effective in photosynthesis, blue-violet less so, and yellow-green of little or no value. The spectroscopic examination of chlorophyll shows that it absorbs the light of just those wave lengths which are most effective in photosynthesis. The close agreement between these diverse lines of evidence strongly suggests that chlorophyll has a two-fold function in photosynthesis. First, it absorbs certain wave lengths of light; second, it transforms this light into forms of energy which are effective in the chemical reactions involved in combining water and carbon dioxide in the production of carbohydrates.

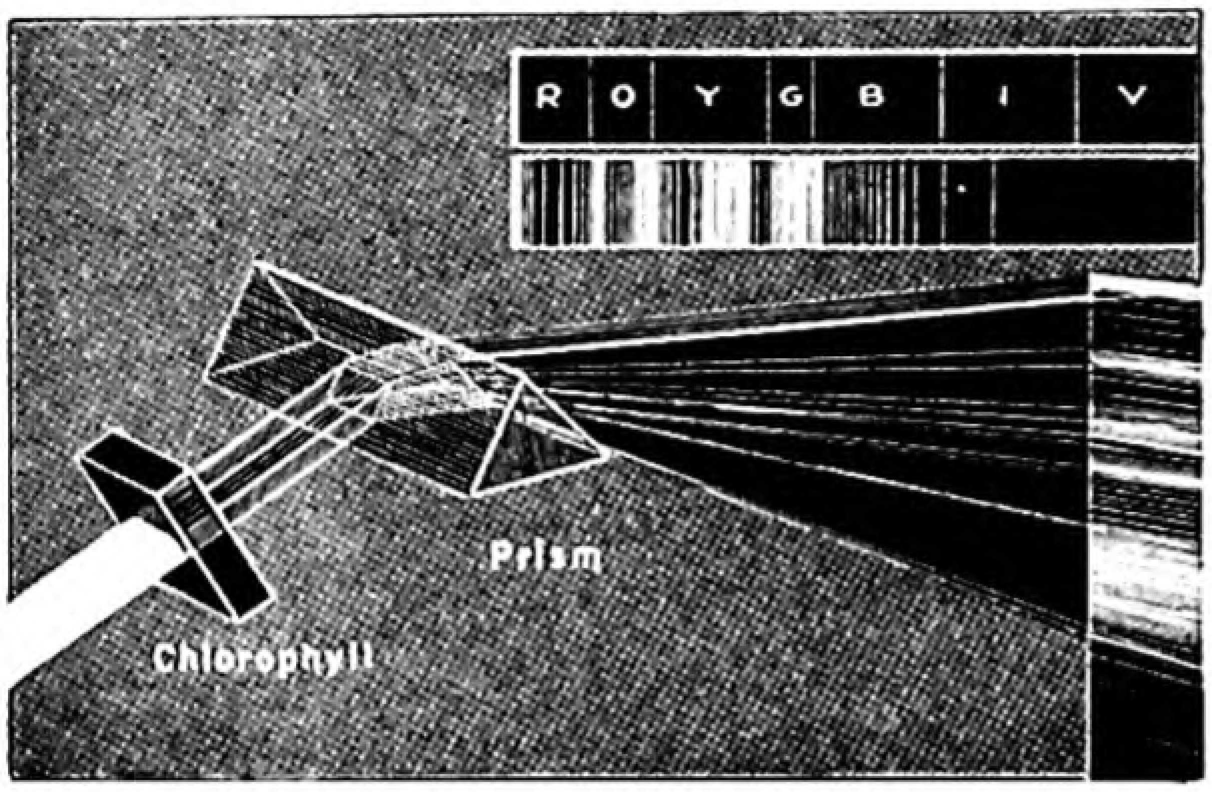


Diagram illustrating the principle of the spectroscope showing a normal solar spectrum above, and the absorption spectrum of chlorophyll below.

Water and carbon dioxide contain no energy that is available to plants. Sugars, starches, and related compounds (carbohydrates) are known as energy-supplying foods. It is the energy which they contain, quite as much as the carbon, oxygen, and hydrogen, that gives them their food value. It seems, therefore, that the chlorophyll absorbs light and makes it possible for the chloroplast to put parts of water and carbon dioxide together, incorporating energy at the same time, thereby producing food.

Water, Carbon Dioxide, and Photosynthesis. Numerous experiments have shown that water is taken into the tissues of common plants rooted in the soil through no other parts in appreciable quantities than the young root tips. From these it is conducted to all the living cells, even to those in the leaves.

Carbon dioxide, on the other hand, is absorbed chiefly from the air by the leaves. In 100,000 parts by volume of out-of-door air there are only 28 to 30 parts of carbon dioxide. From this astonishingly low concentration comes most of the carbon that is built into the structure of the plant and that constitutes more than a third of the dry weight of all foods of both plants and animals.

Carbon dioxide, which is a waste product of respiration, may be used within the plant which forms it. At times, when photosynthesis is taking place, this material may be recombined into carbohydrate before leaving the cells in which it is formed. In a way this action ought rather to be considered the salvaging of refuse and its re-use for constructive purposes.

Oxygen, the Second Product. Beginning with the definition of photosynthesis given on p. 19 the discussion of that process has progressed point by point, and has now reached the oxygen which is released into the air.

Oxygen makes up about one-fifth of the volume of the air, and photosynthesis is almost the only activity in nature that contributes measurably to that oxygen supply. Therefore, if photosynthesis were to cease, the various processes in nature that use oxygen, such as the myriads of chemical oxidations that are continually taking place in the soil, the burning of fuels and the respiration of living organisms would soon exhaust the oxygen of the atmosphere. Then, obviously, life as we know it would cease. *Photosynthesis is fundamental to life, not only in the production of food, but in supplying to the air the oxygen that is required in maintaining life.*

The foregoing discussion of the factors involved in photosynthesis may be summarized in the form of the following outline:

Materials used: Carbon dioxide and water
Agency: Chlorophyll
Energy: Light
Products: Simple sugars and oxygen

The Formation of Starch. In carrying out laboratory experiments on photosynthesis it is customary, by means of hot alcohol, to dissolve the chlorophyll from leaves that have been in the light. By treating them with a dilute solution of iodine they take on a bluish color. This is a standard test for starch. If, on the other hand, the leaf has been in the dark for some days, the blue color does not appear. The interpretation of these observed facts is somewhat involved but is very important. The carbohydrate first produced in photosynthesis is usually some kind of sugar. The sugars, however, are difficult to demonstrate by simple means. Because the chloroplasts are known quickly to transform sugar into starch during photosynthesis, the iodine test is commonly used to show the manufacture of carbohydrates. In reality the production of starch is a step after photosynthesis, but under the conditions found in leaves, the presence of starch is a proof that photosynthesis has been taking place. The contrary statement, however, does not hold true, for the absence of starch does not mean necessarily that photosynthesis has not been occurring, because a considerable number of plants change sugar to starch little or not at all. Such plants as sugar beets, sugar cane, sorghum, sweet corn, most of the meadow grasses, and even onions make starch only feebly. "Sweet and luscious grass" is much more than a mere figure of speech. It is a statement of fact.

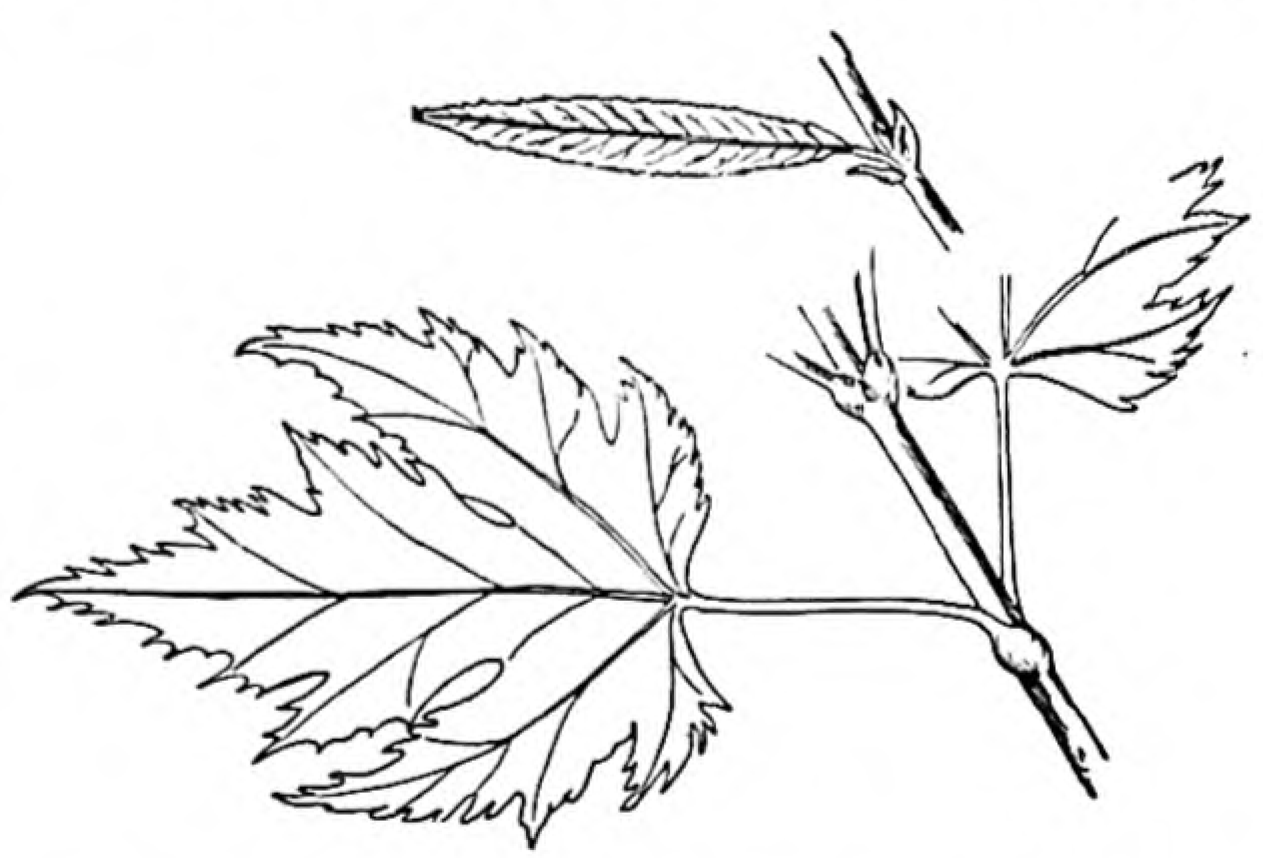
LEAF STRUCTURE AND PHYSIOLOGY

The Leaf as a Photosynthetic Organ. Any part of a plant that is supplied with water and carbon dioxide and which contains chlorophyll so located that it can be reached by light, may carry on photosynthesis. Even cells that lie rather deep within massive stems probably meet these conditions to some extent. It is doubtful, however, if sugar sufficient to be of consequence is produced under these conditions because light that has passed through several outer layers of cells is likely to be too dim to permit more than minimal photosynthetic action.

Of all plant structures, the broad, flat, comparatively thin blade, characteristic of the leaves of a very large number of plants, is the most efficient organ of photosynthesis in existence. It is so constructed that a great deal of surface in proportion to its actual volume is exposed to air and light, and it is thin enough to permit ample light to reach almost every cell. In addition, its internal structure is so organized that carbon dioxide and water can reach every cell in a remarkably efficient manner as the illustration on p. 26 shows.

Parts of a Leaf. Leaves of spermatophytes (p. 3) assume many shapes and since these plants are of special importance to human welfare and are better known than others, discussion will be limited to them.

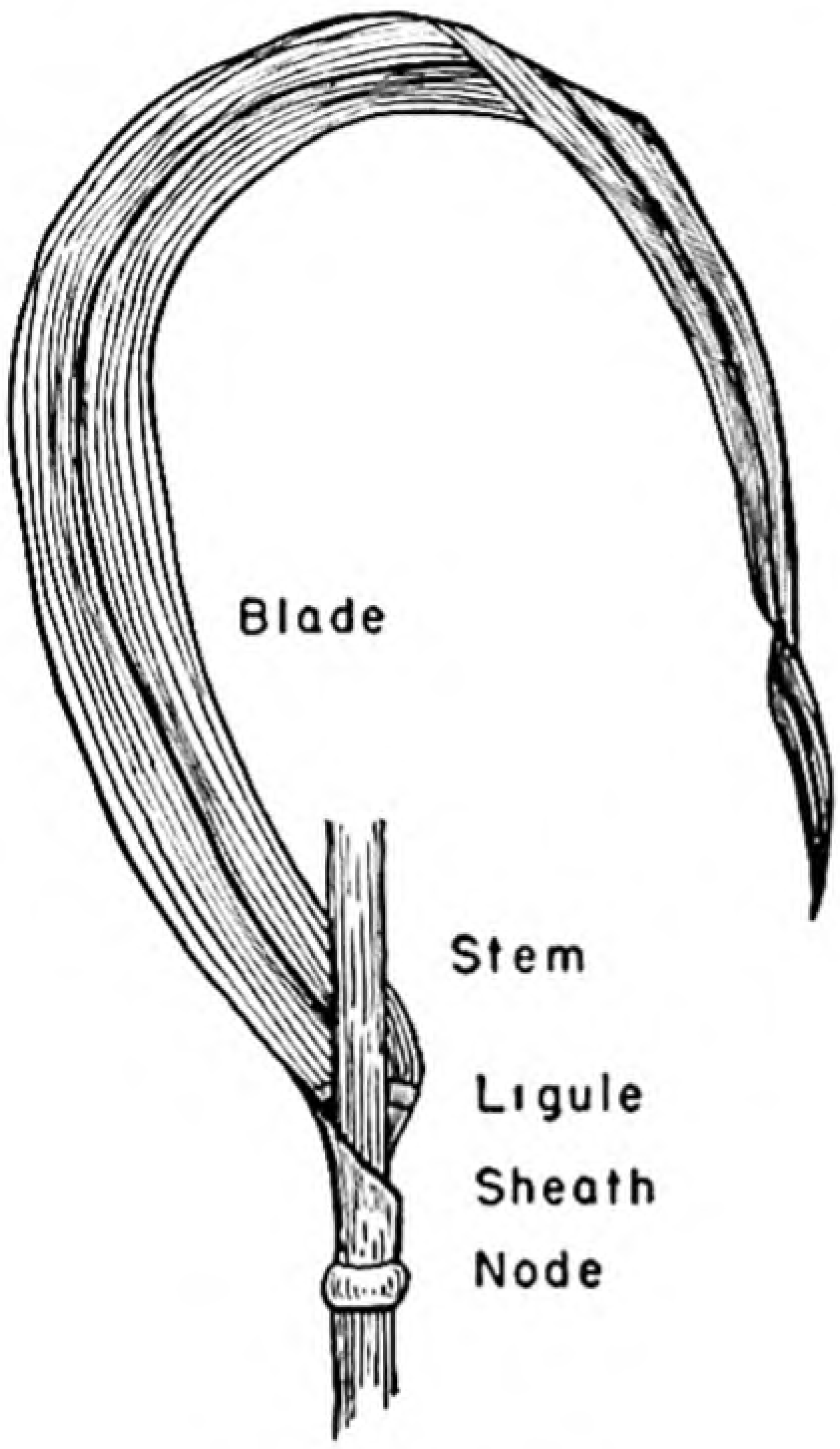
There are two major branches of the seed plants; the gymnosperms, represented in this country chiefly by such cone-bearing trees as the various pines, hemlocks, spruces, firs, sequoias, cedars, and junipers; and the angiosperms. The angiosperms, in turn are subdivided into monocotyledons (single seed leaf) and dicotyledons (two seed leaves). The leaves of plants belonging to each of these three categories are, with few exceptions, quite distinctive. Since a dicotyledon leaf includes



Parts of leaves of dicotyledons. (*Top*) Black willow showing blade with midrib and veins. At base of blade is a short petiole with two laterally attached stipules. A bud is just above the base of the petiole. (*Bottom*) Silver maple. The midrib is replaced by three main veins. There are no stipules.

almost all the structures found in the other two, it will be described first.

Dicotyledon Leaves. The usual type of thin leaf of a dicotyledon has several rather definite parts. The broad, flat expansion is the *blade*. Almost always there is a network of fine lines extending in all directions in the blade. These are the *veins*. Netted veining is characteristic of dicotyledons.



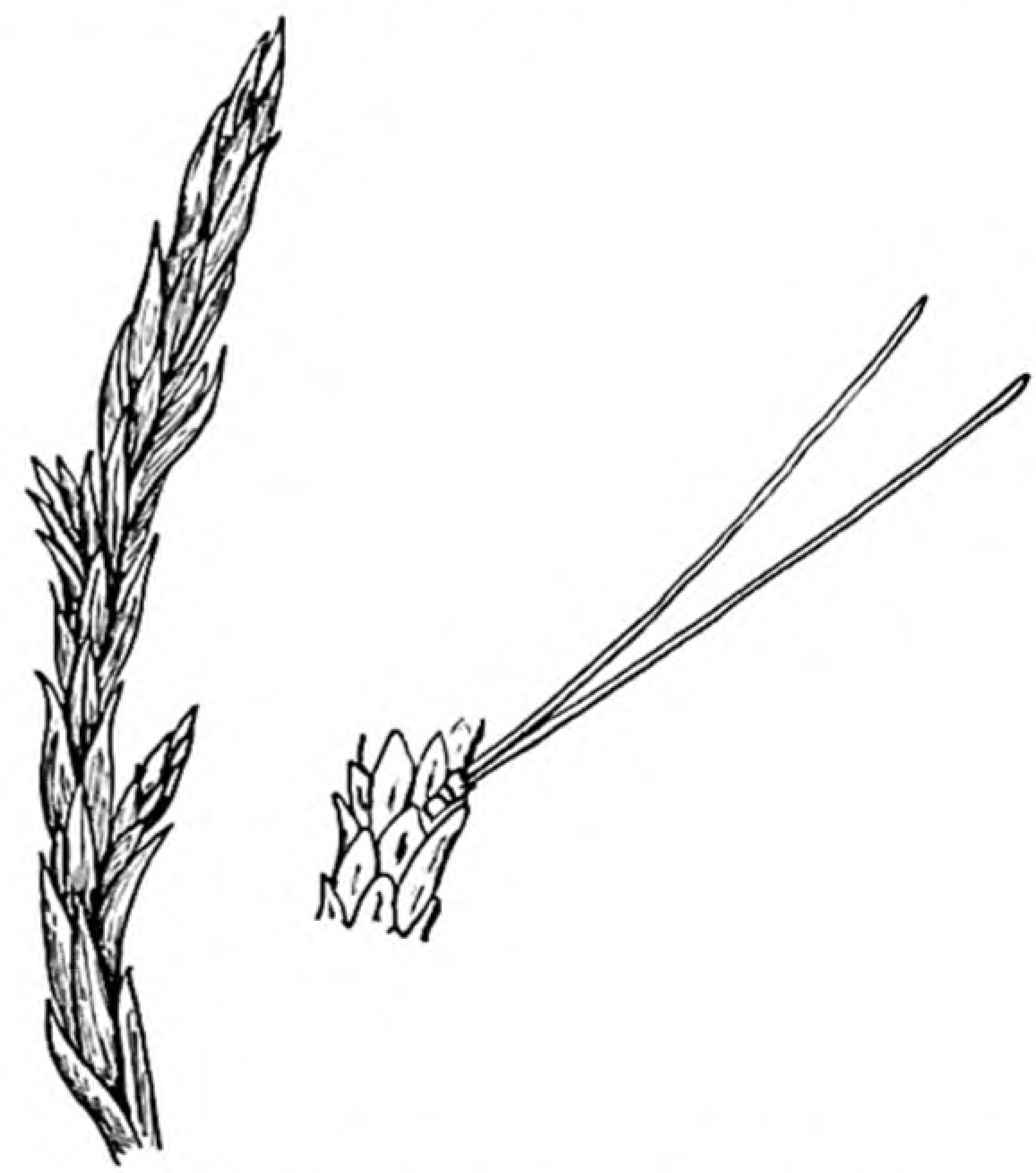
Leaf of grass.

Usually either a large vein, the *midrib*, extends the entire length of the blade or several radiating branches replace it. The system of veins brings water and minerals into the leaf and carries away the foods that are synthesized there.

The blade is usually attached to the stem of the plant by a slender *leaf stalk* or *petiole*. Petioles vary greatly in length in different species, sometimes being very short or entirely lacking. At the base of the petiole, where it is attached to the stem, there are frequently two small appendages which sometimes look like rudimentary leaves. These are the *stipules*. They are conspicuous in such plants as the geranium, violet, pea, and some of the willows. In a few plants they are represented by a pair of thorns or of tendrils. The leaves of a majority of plants have no stipules, and in a considerable number they are present when the leaf is young but soon fall off.

Not only are petioles and stipules sometimes entirely lacking, but in some kinds of plants even the blade may be so narrow as to be practically absent. This last condition is common in plants of the deserts, where leaves are frequently little more than narrow, fleshy cylindrical extensions from the stems, each with a single unbranched vein extending throughout its length.

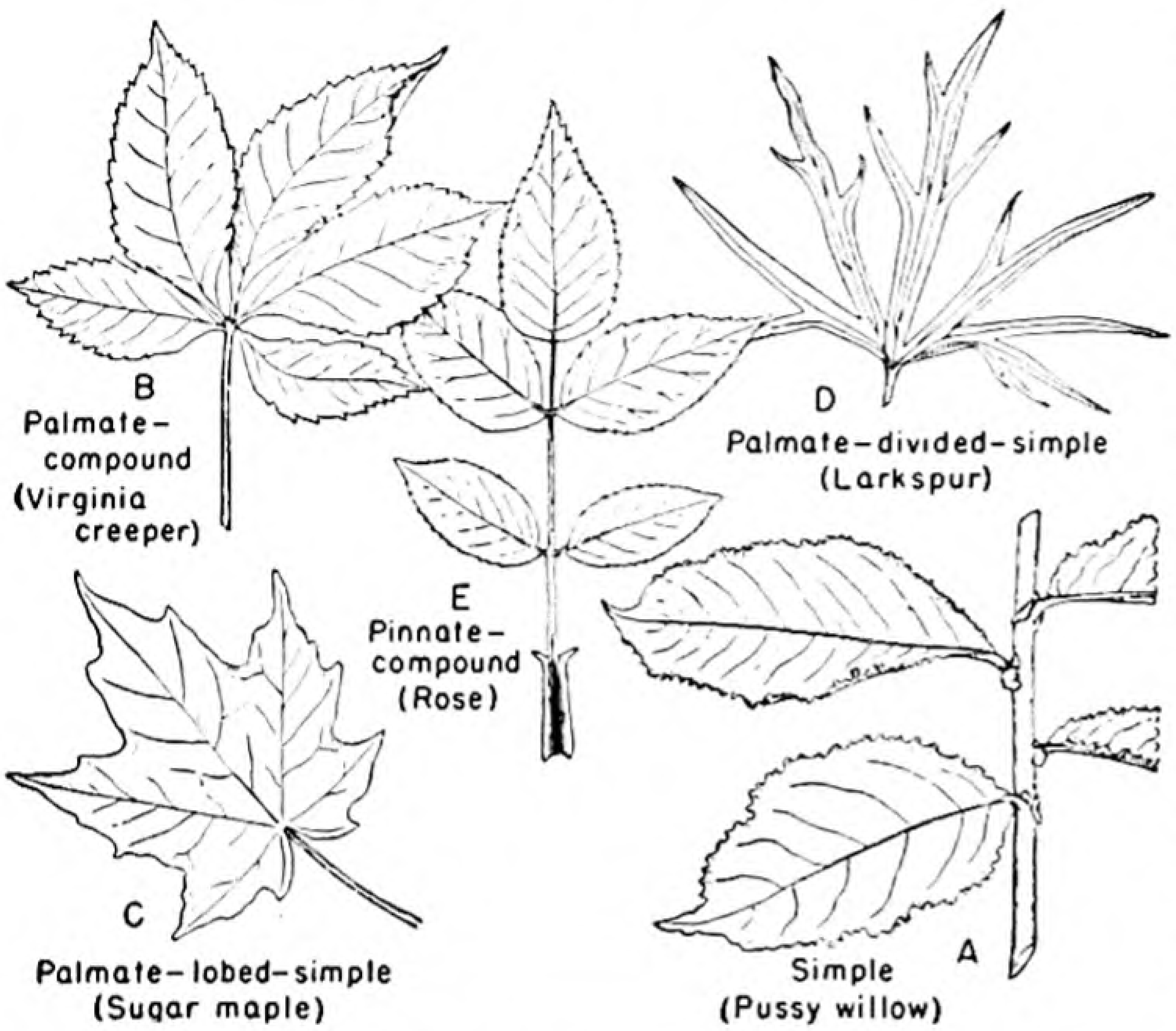
Monocotyledon Leaves. The grasses and other monocotyledons very often have a rather well-developed midrib with veins extending parallel with it throughout the length of the blade. Sometimes, as in the leaf of such plants as bananas, or cannas, the veins are parallel with each other but extend away from the midrib at a wide angle. In others, as in the onion, there is no midrib. In all of these, however, the parallel veining characteristic of the monocotyledons is evident.



Leaves of conifers. (*Left*) Twig of juniper with numerous scale leaves. (*Right*) Two needle-shaped leaves of pine.

In the grasses, the blade arises, not from a petiole, but from a *sheath* which is a thin structure that enwraps the stem. At the place where the sheath merges with the blade there is usually a more or less definite collarlike extension called the *ligule*.

CONE-BEARING GYMNOSPERMS. In the Orient, in the Tropics, and in the Southern Hemisphere there are groups of gymnosperms, seldom met with here, with rather angiospermlike leaves. The cone-



Simple and compound leaves.

bearing gymnosperms (conifers) to be seen in most parts of North America, however, have peculiar, hard leaves that sometimes are long and slender and sometimes take the form of small scales on the twigs. In either case the leaves are very narrow, having no blades.

Forms of Leaf Blades. The leaves of the majority of well-known angiosperms, as has been said, have definite blades. The leaf is *simple* if the blade is not divided into distinct parts, and is *compound* if it is so divided. The divisions of compound leaves are often called *leaflets*. In many instances the blade is more or less deeply divided but not into separate leaflets. In this case it is said to be *lobed*, but is considered to be simple.

If a compound leaf has leaflets, all arising from the summit of the petiole, radiating out like the fingers from the palm of the hand, it is said to be *palmately compound*. Virginia creeper, buckeye, and clover are good examples. In contrast, leaves are *pinnately compound* (*pinna*, feather) if the leaflets arise along an axis or *rachis* as in the walnuts, hickories, ashes, locusts, box elders, peas, and some palm trees.

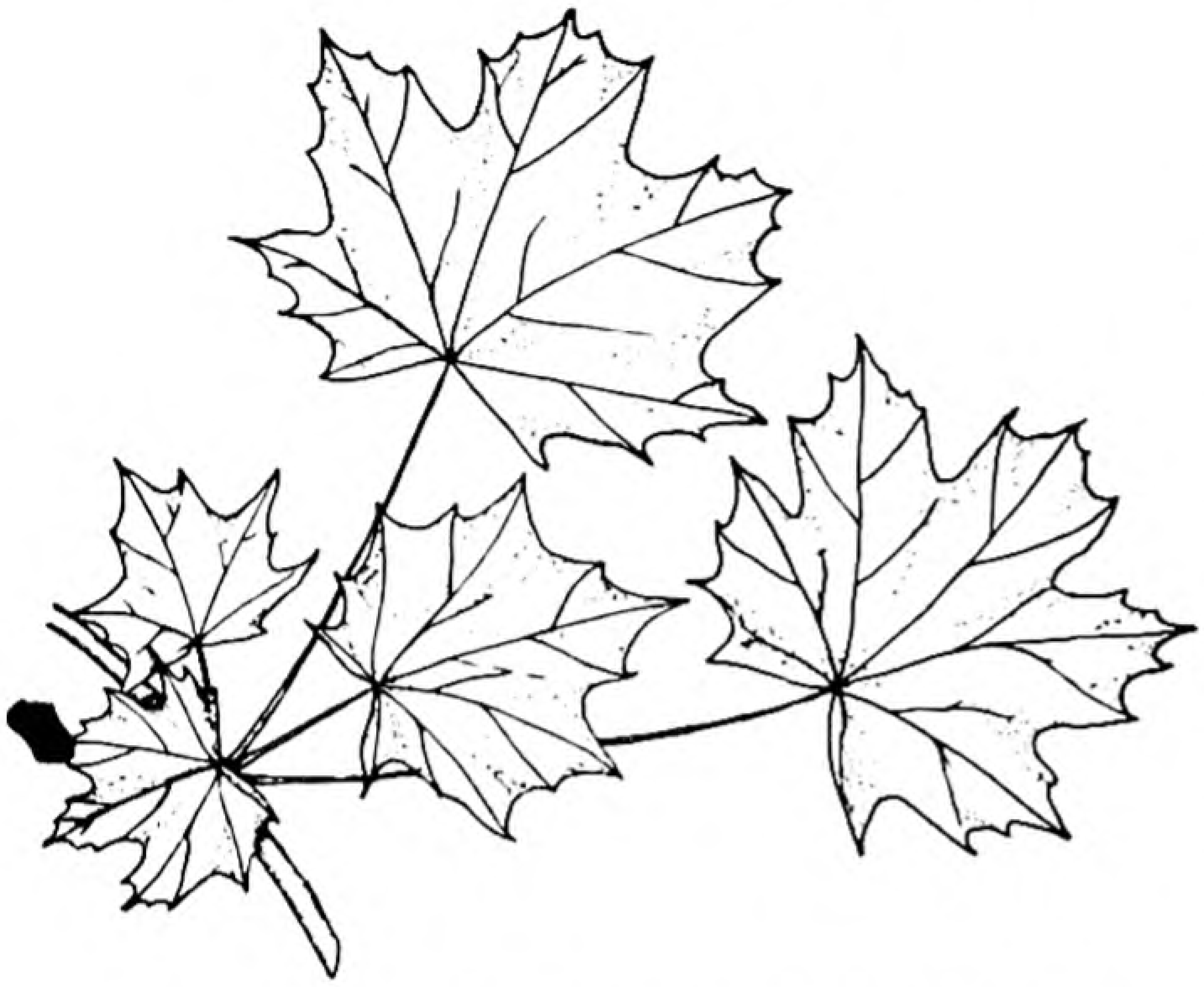
Leaf Mosaics. The leaves of an ivy climbing a tree trunk or a wall, assume such positions that they shade each other very little while often almost entirely hiding the space over which they are growing. Likewise, the shade under many broad-leaved trees is so complete that only a little sunshine reaches the ground. Close examination shows the leaves to be attached at the outer ends of the branchlets and to be so placed that they cast little shade on one another. Such an arrangement is called a *leaf mosaic*.

The position assumed by the leaf blades results from the bending, twisting, and differential lengthening of the petioles, bringing the upper surface of each leaf into such a position that it faces the strongest illumination.

Structure. Leaves of plants with the hereditary capacity to thrive in water, in moist soil, and in deserts vary greatly in microscopic anatomy. Like-

Leaf mosaic of ivy growing on a building.

wise, there is much inherent diversity between the cellular arrangements of the leaves of monocotyledons, dicotyledons, and many of the gymnosperms, even when they are growing together in similar



Leaf mosaic of sugar maple showing placement of blades by different lengths and directions of petioles.

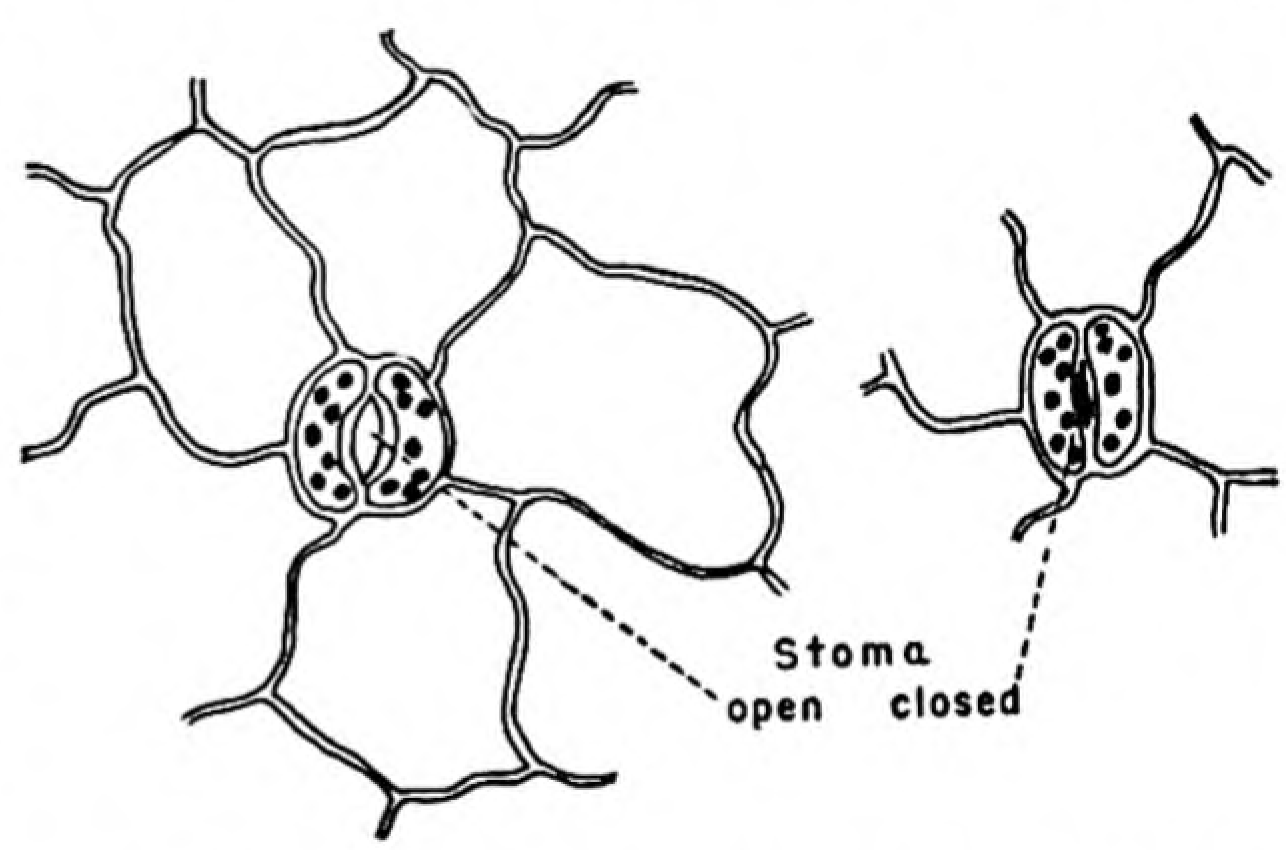
surroundings. Also, in some species structure is greatly influenced by the environment. As an example, the shaded and the strongly illuminated leaves of the same plant sometimes are very different from one another. It is, therefore, impossible to choose a single kind as a typical example by which to illustrate all leaf anatomy. Nevertheless, these structures can best be understood by means of a thorough acquaintance with one type followed by comparisons with others. The leaf of an ash tree is satisfactory to begin with. It is fairly representative of the leaves of dicotyledons that live in moderately humid climates.

Leaf of Ash Tree. All leaves of seed plants have an outside layer of cells, the *epidermis*. These cells are usually wavy and irregular in outline as seen in surface view, but all are securely attached to their neighbors, making a continuous covering over the cells of the interior of the leaf. In the case of many plants, and the ash tree is no exception, a waxy secretion, the *cuticle*, forms a waterproof, varnish-like coat over the outside of the epidermis. Both the epidermal cells and the cuticle over them are transparent, freely admitting light.

Through the lower epidermis of ash leaves there are numerous definite openings, the *stomata* (singular, *stoma*, meaning mouth), each framed by a pair of specialized cells, the *guard cells*. The stomata allow the air in the intercellular spaces inside the leaf to have contact with that on the outside. Without such openings it would be impossible for carbon dioxide of the air to reach the chlorophyll-bearing cells within the leaf and photosynthesis could not take place. Changes in the shapes of the guard cells cause the openings to become larger or smaller, or even to be completely closed in response to external conditions.

The epidermis entirely encloses the interior of the leaf. Although it is proper to refer to the upper and lower epidermis it should be understood that these two form a continuous layer, merging with each other at the leaf edges.

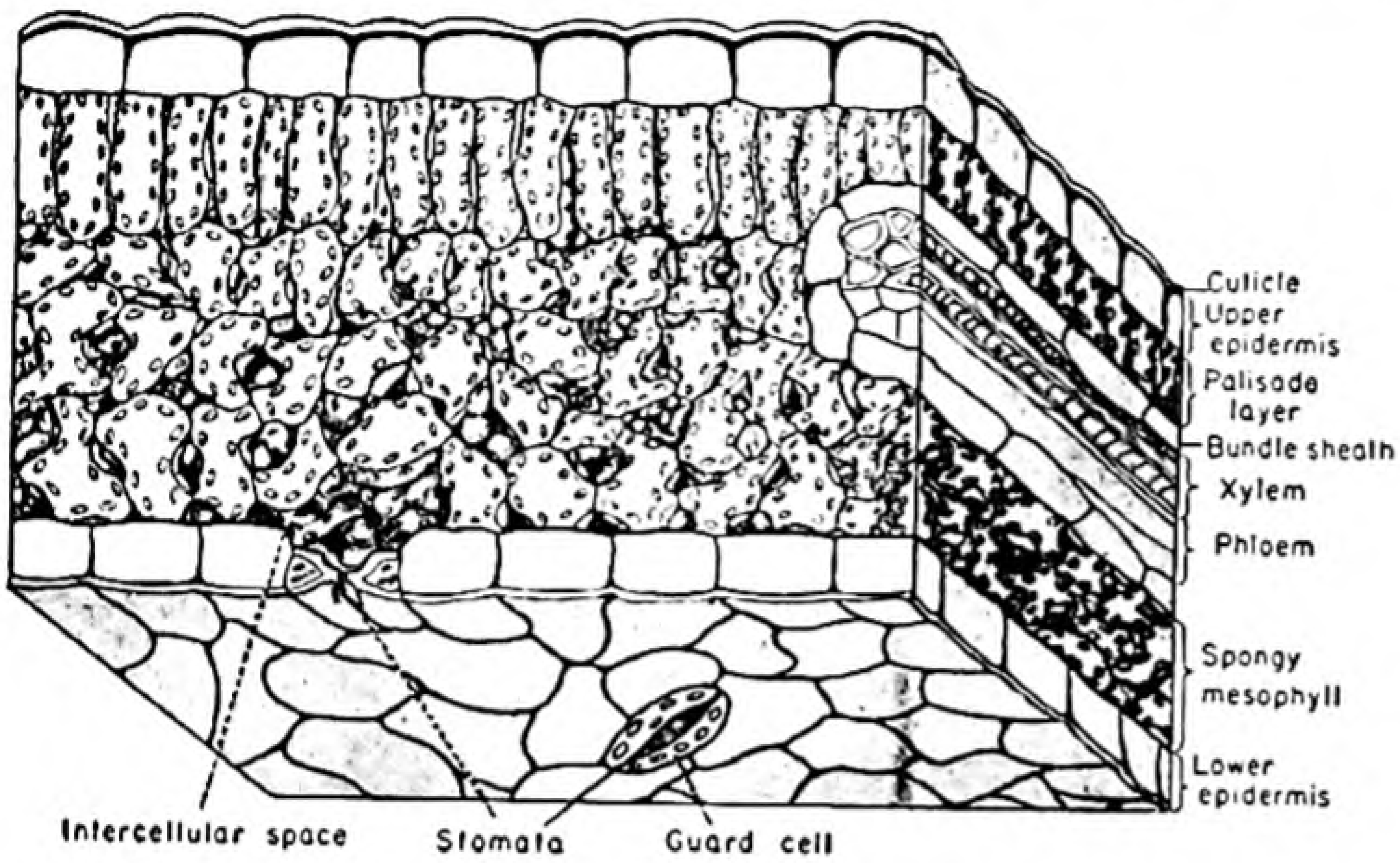
Enveloped within the epidermis, the cells containing chloroplasts make up most of the inside of the leaf. These chlorophyll-bearing cells are commonly known collectively as *mesophyll* (*mesos*, middle; *phyllon*, leaf). The long mesophyll cells arranged at right angles to the upper epidermis



Epidermis with stomata in surface view. The kidney-shaped guard cells surround the stomatal openings. The large, irregular cells constitute the epidermis.

constitute the *palisade tissue;* the cells of irregular shape next to the lower epidermis make up the *spongy mesophyll*. Throughout the interior of the leaf there are numerous air spaces. These are especially

conspicuous in the spongy mesophyll and are continuous with the outside air through the stomatal openings. Notwithstanding the loose arrangement of the cells of this tissue they have very definite connections between them. This whole structure is to be regarded as a peculiarly organized meshwork of cells rather than as a collection merely piled loosely together.



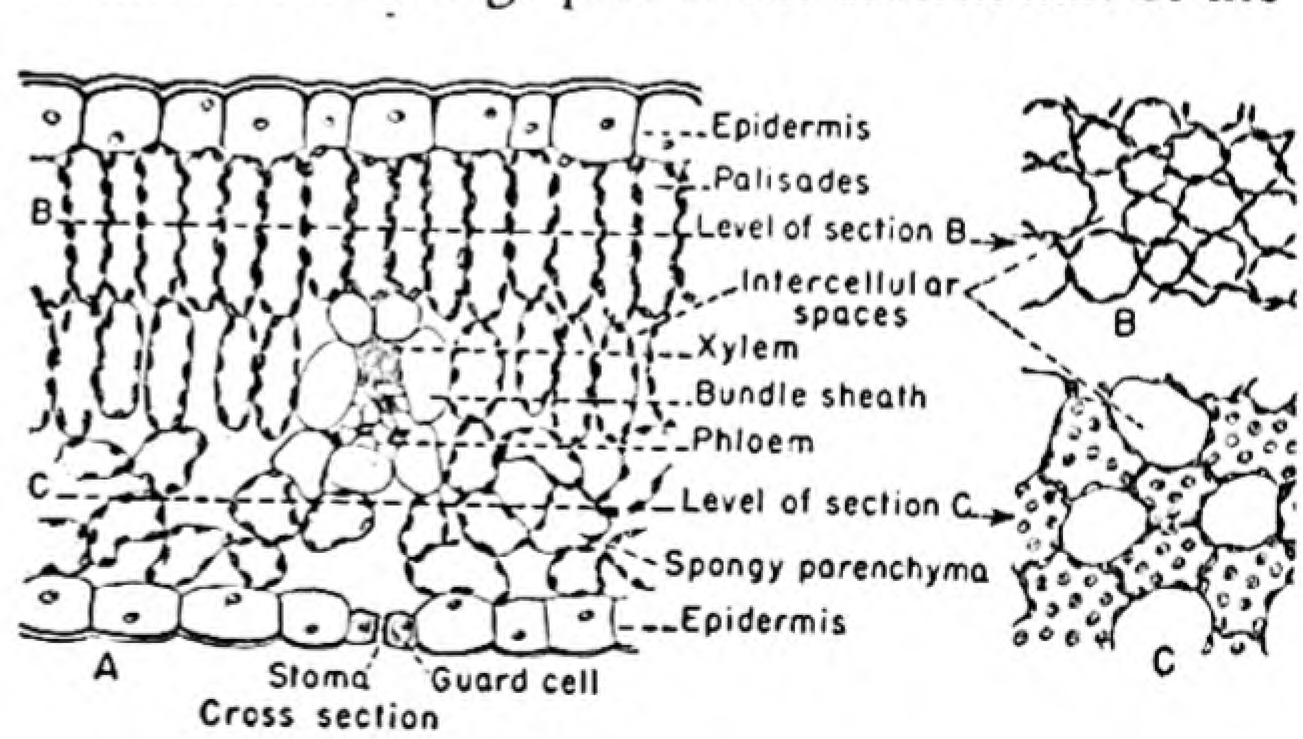
Three-dimensional drawing showing structure of dicotyledon leaf.

The air spaces within the palisade tissue are not clearly shown in the cross section of a leaf because they are obscured by the long, narrow, parallel cells. These intercellular spaces are shown better in B of the accompanying illustration, which is made from a section cut parallel to the upper epidermis, and consequently at right angles to the long axes of the palisade cells.

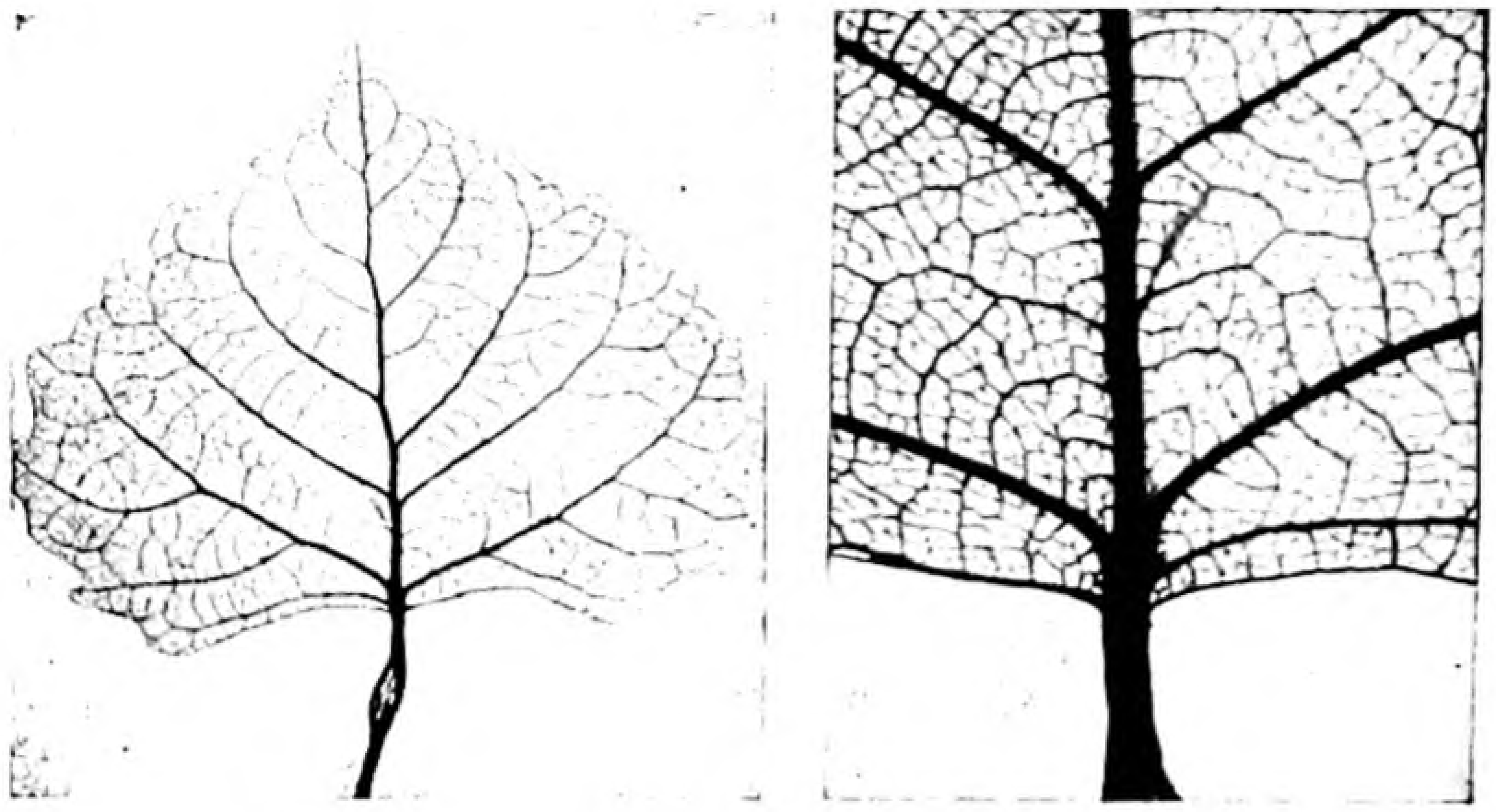
Besides the epidermis and mesophyll, the cross section shows also the structure of the veins of the leaf. These are really *vascular bundles*, and a more detailed description of them will be given in Chapter 8. In the leaf, a vascular bundle is made up of three parts: an outer sheathing layer, usually one cell thick, the *bundle sheath*, and two masses of conductive tissue, the *xylem* and *phloem*. In the larger veins there are also considerable numbers of thick-walled strengthening cells which help to give support to the leaf blade. The xylem and phloem can usually be distinguished from each other by the thickness of their cell walls. The xylem is the part toward the upper epidermis and its cells have thicker walls than those of the phloem, which is toward the lower epidermis. There is a more or less distinct division of labor between these two tissues. The xylem distributes water and dissolved materials to all parts of the leaf, and the phloem carries away the sugars and proteins which are synthesized there.

A close examination of a fresh leaf of almost any dicotyledon held up to the light shows that the veins divide and subdivide, making a network, and are so distributed that no part of the mesophyll is far removed from one or more veinlets. The fine divisions of the veins are better shown in preparations made by destroying the softer parts, leaving only the xylem or woody skeleton. The illustration on p. 27 shows also that there is a very intimate contact between a veinlet and the mesophyll cells. This direct connection is necessary if the chlorophyll-bearing cells are to receive water from the xylem and if the phloem is to carry on its function of transferring synthesized foods from the mesophyll to other parts of the plant.

LEAF OF BLUEGRASS. Kentucky bluegrass thrives best under about the same climatic conditions as those in which most species of ash trees grow. It is common over a large part of the eastern half of the United States and is used as a lawn grass in many other sections of the country where rainfall or irrigation make growth conditions suitable. Probably no grass is so widely known as this one. It is



Sections through blade of ash leaf. (A) Cross section. (B) Section across palisades. (C) Section through spongy parenchyma cut parallel to lower epidermis.



Skeletonized leaf of cottonwood, showing network of veins and veinlets.

therefore suitable to use as a representative of the monocotyledons.

A cross section of a blade of a leaf shows several characteristics that contrast with those of the ash leaf. Two of these relate to the epidermis. First, the stomata are all in the upper epidermis; second, extending along either side of the midrib is a narrow band of specialized epidermal cells, the *bulliform* cells. These are so constructed that when the leaf begins to wilt they tend to collapse, closing the two halves of the leaf together like the pages of a book. This action has the effect of bringing the two stoma-bearing surfaces together, probably resulting in somewhat reduced loss of water vapor from the leaves.

The mesophyll has no elongated cells, like those of the palisade layer. Instead, it is made up of a spongy tissue, containing extensive intercellular spaces.

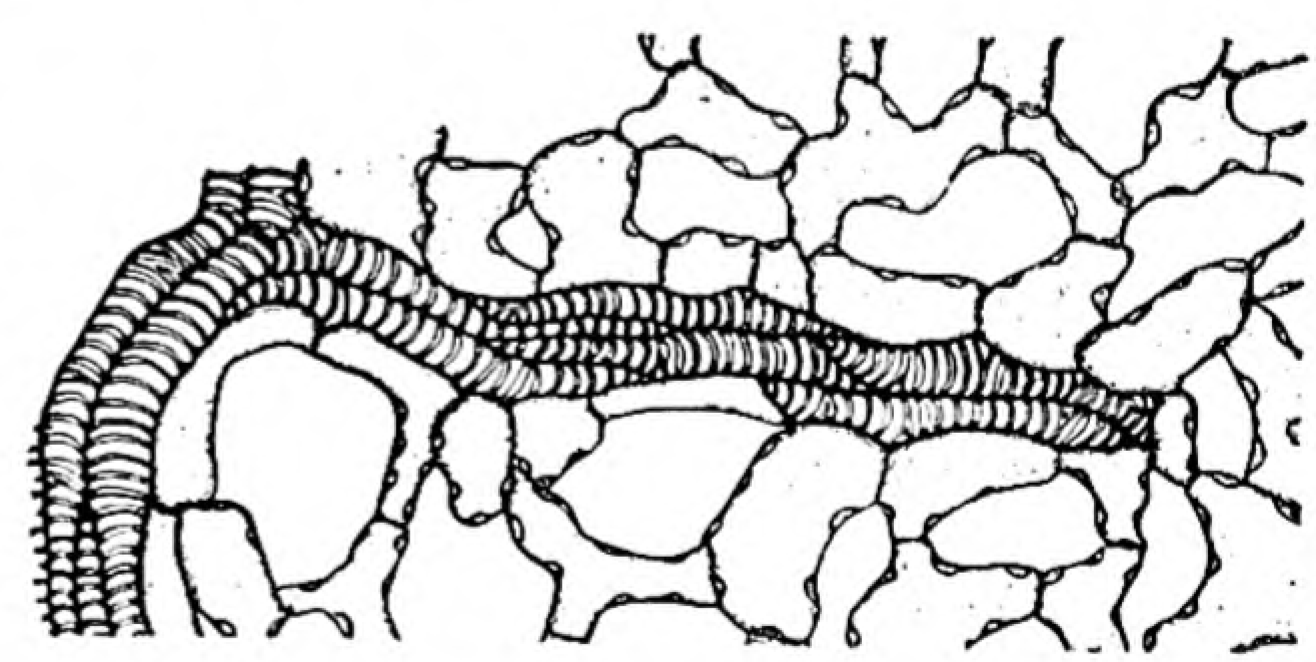
The veins of the bluegrass leaf are parallel with each other, as is usual in monocotyledons, but in cross sections they are found to be organized much like those of the ash tree.

LEAF OF WHITE PINE. If, by contrast with the leaf structures just described, a study is made of those of the white pine tree, a gymnosperm native of the humid Northeast, still other peculiarities appear. First of all, it will be noted that these needlelike leaves do not have true blades. Instead, when seen in cross section, each of the five leaves that grow together in a small bundle has a form closely approaching a triangle, with one side somewhat rounded. The walls of the epidermis are extremely thick—so thick, in fact, that there is little room left for protoplasm—and the surface is covered with a layer of cuticle. The stomata may be seen in the two flat sides of the triangular leaf section. The guard cells are depressed considerably below the surface of the epidermis. Actually, they are attached to the bottoms of grooves which extend throughout the length of the leaves.

Just underneath the epidermis there lies a layer of cells with thick, tough walls. These are strengthening cells or *sclerenchyma*.

The mesophyll is constructed largely of chlorophyll-bearing cells with peculiar extensions of the cell walls which separate the protoplasm into thin layers. These peculiar cells are often called "arm palisades." The function of these infolded walls, if, indeed, they have a function, is only a matter of conjecture. No adequate explanation has yet been given for their presence.

Air enters the leaves through the stomata and a series of intercommunicating intercellular spaces allows it to circulate freely among the cells of the mesophyll, permitting those exchanges necessary to the process of photosynthesis.

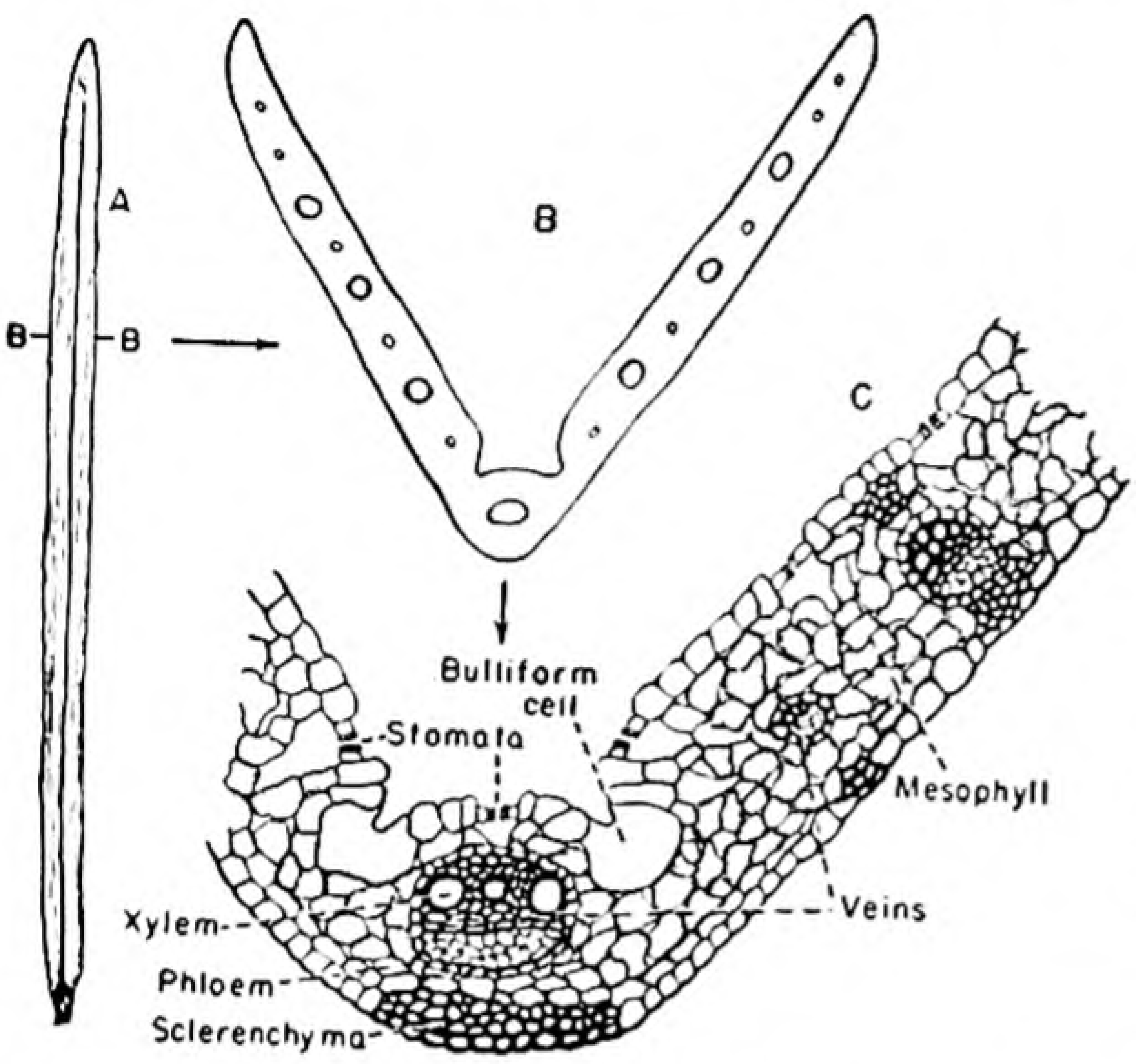


Drawing of smallest veinlets of leaf showing xylem elements surrounded by cells of spongy parenchyma. From section of lilac leaf.

In certain of these leaves there is a single tube near the epidermis. This is the *resin duct*. It is lined with glandular cells which secrete the resin, the

sticky substance familiar to everyone who comes in contact with pine trees.

Throughout the length of the leaf there extends a large vascular bundle constructed, as usual, of



Leaf of bluegrass. (A) Leaf, natural size showing parallel veins. (B) Cross section of leaf, showing veins. (C) Cellular structure.

phloem and xylem. Completely encircling the bundle is an unusually definite bundle sheath.

Leaf Structure and Environment. Plants that grow in water, such as waterlily, pondweed, and cattail are called *hydrophytes;* those in locations where the soil is usually moist and the air humid, such as white ash, white pine, and bluegrass are *mesophytes;* while desert plants and others from dry localities, like creosote bush, mesquite, and yucca are *xerophytes.*

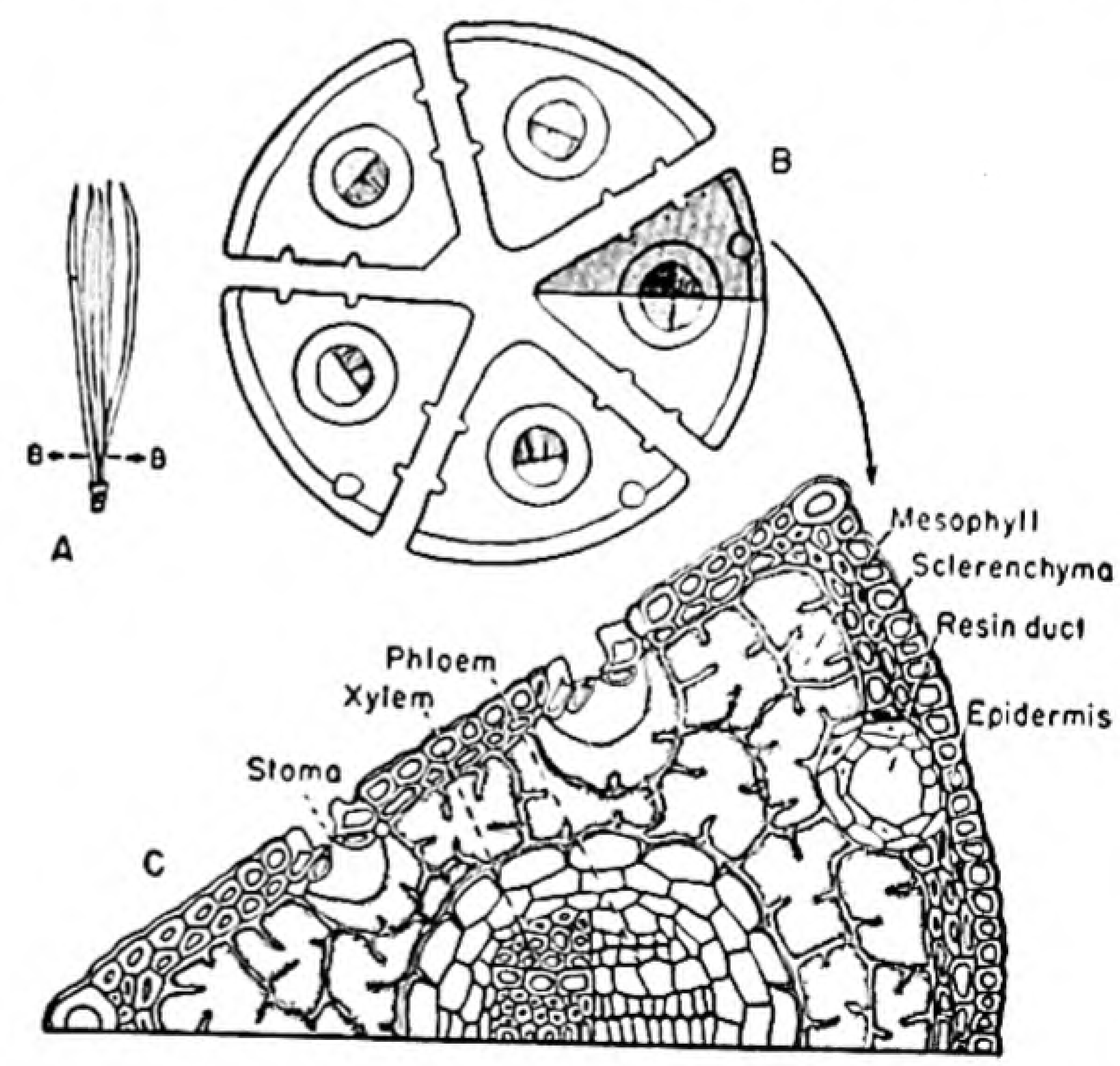
The three plants whose leaves have already been discussed are all mesophytes. Leaves of hydrophytes that grow completely covered with water usually are little more than very loose spongy tissue, surrounded by a layer of epidermis without either cuticle or stomata. On the other hand, leaves of xerophytes very often have remarkable development of palisade tissue. In extreme cases the entire mesophyll is constructed of palisade cells. In some species, but in by no means all, xerophytes have a remarkably thick cuticle.

Summary of Leaf Structure. Primarily, a leaf is a photosynthetic organ. It consists principally of mesophyll, which is a mass of cells containing numerous chloroplasts, and which is surrounded by a protective epidermis and is provided with a conductive and supporting system. A number of peculiarities make it especially effective in carrying on photosynthesis. In the leaves of ordinary land plants, the epidermis is translucent, admitting light; waterproof, resisting loss of water from the mesophyll; and perforated by stomata, permitting carbon dioxide to enter while oxygen escapes.

Stomata are so numerous that, when wide open, they form a very efficient ventilating system for the inside of the leaf, admitting air almost as freely as if no epidermis were present.

The veins and veinlets combine supporting and conductive tissues. Certain cells with thick walls provide sufficient support to display the leaf to the light, the xylem supplies water to all the cells of the leaf, and the phloem carries away the manufactured foods.

The Chloroplast. A microscopic examination of any chlorophyll-bearing plant tissue, such as thin sections of leaves, reveals the fact that the



Sections of white pine leaves. (A) Bundle of leaves. (B) Semi-diagrammatic drawing of section through the five leaves that compose a bundle. (C) Cellular structure.

green color occurs in small, rounded bodies. These are chloroplasts (*chloros*, green; *plastos*, that which is formed). The broad leaves of certain mosses or those of *Elodea*, a common floating water plant

that is often grown in fish bowls, are very convenient for such studies. If the chloroplasts are first examined and then the leaf is treated with hot alcohol, it is found that the green color gradually disappears. In the places where the chloroplasts have been, there remain small, clear bodies of specialized cytoplasm. Each of these is called a *stroma* (plural, *stromata*). Further analysis shows the coloring material to be made up of at least four separate pigments. Most evident of these are two green substances called *chlorophyll a* and *chlorophyll b* (*chloros*, green; *phyllon*, leaf). A third, deep orange in color, is called *carotin*, because it is the characteristic pigment in the roots of carrots. The fourth is known as *xanthophyll* because its color is yellow (*xanthos*, yellow). The two chlorophylls are chemically closely related to one another and, likewise, carotin and xanthophyll have much the same structure. The following formulas will amplify this statement:

Chlorophyll *a*	$C_{55}H_{72}O_5N_4Mg$
Chlorophyll *b*	$C_{55}H_{70}O_6N_4Mg$
Carotin	$C_{40}H_{56}$
Xanthophyll	$C_{40}H_{56}O_2$

It is interesting to note that hemoglobin, the red coloring material of the blood of higher animals, is closely related chemically to chlorophyll, the green coloring matter of plants. An atom of magnesium occupies a central place in the chlorophyll molecule and iron is similarly situated in hemoglobin. Because of this similarity, there is much speculation concerning the possible manufacture of hemoglobin from chlorophyll within the body of the animal. Thus far, however, there is no proof of such a transformation. Carotin, on the other hand, is known to be the source of vitamin A, which is extremely important to animals. The four plant pigments are sometimes referred to as the chlorophyll-carotinoid complex. Plant parts that are dark green are relatively rich in the chlorophylls, and those that are yellowish green are abundantly supplied with carotin and xanthophyll. These color differences may be seen if leaves from many kinds of plants are placed side by side for comparison. But whatever the comparative amounts, chlorophyll seems never to be produced free from carotinoids.

By way of summary, a chloroplast is composed of:

Stroma
Chlorophyll *a*
Chlorophyll *b*
Carotin
Xanthophyll

There are other plants or parts of plants which have no chlorophyll at all. Examples are seen in bleached celery, in roots or other underground parts, and in the petals of many flowers. Microscopic examination shows that in many of these the stromata of what would ordinarily be chloroplasts are present, but they do not produce chlorophyll. Stromata without pigments are often called *leucoplasts* (*leukos*, white). In other cases xanthophyll and carotin may be formed without chlorophyll, giving a yellow color to the part concerned. The color bodies thus produced are known as *chromoplasts* (*chroma*, color). Chromoplasts of this kind are common in the yellow petals of flowers and in the roots of carrots. Because chlorophyll is absent, photosynthesis does not occur in the yellow chromoplasts or in the colorless stromata of the rudimentary or modified chloroplasts.

When a seedling emerges from the ground, its young developing leaves are usually white, or more often are somewhat yellowish. But light in some way stimulates protoplasm to produce carotinoids and chlorophyll in the stromata, making them into chloroplasts. Therefore, the leaves soon become green. In this series of color changes any individual plastid is first a leucoplast (stroma); it then becomes a yellow chromoplast; and finally, it is a chloroplast.

How Carbon Dioxide Enters a Leaf. A company of visitors comes into a closed greenhouse on a sunny day and spends an hour. If tests are made they show that there is a rapid rise in the carbon dioxide content of the air during this time. This gas comes from the human breath which is a very rich source of carbon dioxide. The company leaves and a succession of tests shows that there is a rapid decline in the carbon dioxide concentration in the air and soon it approaches very close to zero.

If this same visit had occurred at night, the high concentration would have remained but little changed until morning. Obviously, the reason for this situation is that in the daytime photosynthesis by plants takes place, using carbon dioxide, while at night it does not. But the question remains as to what forces bring the carbon dioxide into the leaves. Before an adequate answer can be given to this question, it will be necessary to have a clear picture of the process of *diffusion*.

DIFFUSION. This process may be illustrated by many common experiences. Suppose ether is spilled in a classroom. Soon, students in adjoining rooms become aware of its presence through the sense of smell. This means that the vapor has actually moved through the air from one room to another. It has, in fact, traveled in all possible directions from the place of its greatest concentration to those places of its lesser concentration. If, at the same time, a small quantity of chlorine gas is set free in another room nearby, it follows the same physical laws and in so doing enters the room where the concentration of ether was greatest but where there was no chlorine.

These examples illustrate two very important facts of diffusion: First, *any diffusing substance travels from regions of higher to those of lower concentration of itself*, and second, *in a mixture of gases, each follows its own direction and rate of diffusion, irrespective of the others*. These two forms of behavior serve rapidly to equalize any local disturbances that may occur in the concentration of gases. These simple illustrations give little idea of the remarkable energy that carries rapidly diffusing substances from place to place. It has been shown that molecules of oxygen at usual temperatures travel at the rate of about 600 miles per hour. It should be clear that in such a mixture of gases as air—made up chiefly of molecules of nitrogen and oxygen all exhibiting great energy of motion, dashing about, colliding, rebounding, and glancing off each other—diffusion is actually a violently active process.

DIFFUSION THROUGH STOMATA. To understand the forces which cause carbon dioxide to enter a leaf, it is only necessary to apply certain facts already encountered. A leaf is surrounded by air, and the spaces in its loose, porous interior are filled with air. These two atmospheres, one inside the leaf and one outside, are connected through the stomata. As the carbon dioxide in the intercellular spaces is used in photosynthesis, more of it, traveling from its place of greater concentration outside the leaf, speedily diffuses in through the stomata. At the same time, the oxygen thrown off enriches the inner atmosphere and therefore diffuses outward.

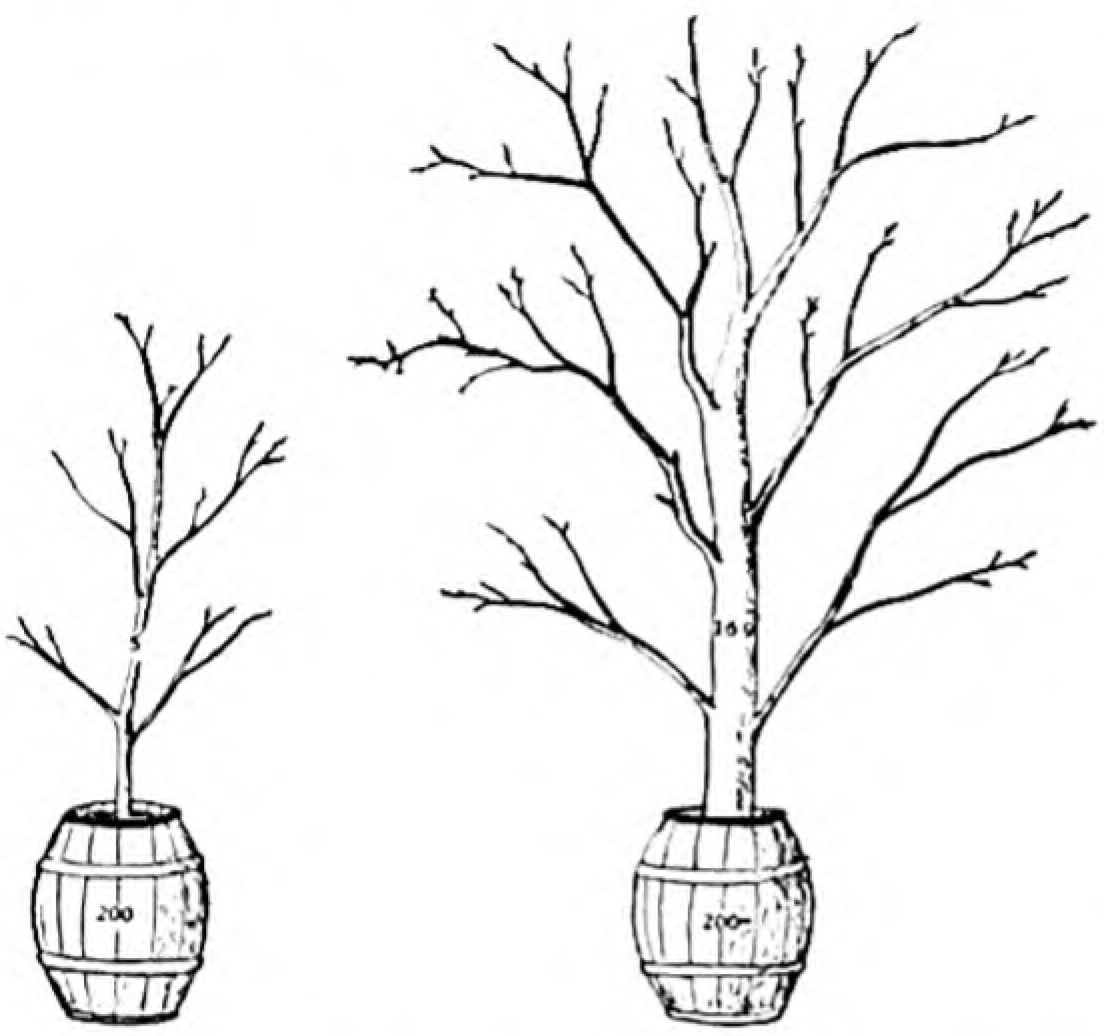
DIFFUSION THROUGH THE PLASMA MEMBRANE. Even after carbon dioxide has entered the intercellular spaces within the mesophyll it must pass through the cell walls and plasma membranes before it reaches the chloroplasts. In this connection it should be understood that the gases of the air are unable to move in significant amounts through dry cellulose walls. But the cells of living leaves are usually well supplied with water, and both the protoplasts and their surrounding walls are colloidal structures. Therefore, their exposed surfaces are continually wet, much like the surface of a thin jelly. Such gases as nitrogen, oxygen, and carbon dioxide go into solution rather readily in this layer of water. Dissolved substances diffuse in the solvent, following the same laws as are followed by free gases. In this manner both carbon dioxide and oxygen freely enter or leave the cell so long as they are traveling from regions of their higher to those of their lower concentration.

When photosynthesis is taking place at a rapid rate, in what direction does oxygen travel in a mesophyll cell? In what direction does carbon dioxide move under these conditions? In which direction does each of these gases travel if the plant is in the dark?

At this point it will be profitable to return to the question of the forces at work which caused the carbon dioxide to leave the atmosphere in the greenhouse and enter the leaves of the plants. It should now be possible for the student to trace this gas through all the steps from the time it was a part of the human breath until it was used in the manufacture of glucose in the process of photosynthesis.

The Growing Understanding of Photosynthesis. The student who is learning some of the facts that have been discovered by scientists may

fail to sense the importance of the quest and the patient effort by which they have been found out. Scientific research is, in reality, a form of detective work or, sometimes, of exploration, often requring the combined efforts of many investigators.



A repetition of van Helmont's experiment.

The beginning of our knowledge of photosynthesis is a case in point. The earliest recorded investigation that helped to give some clue to an answer to the question of the source of food was made by the Belgian physican Jean Baptiste van Helmont near the beginning of the seventeenth century. In an attempt to answer the old question of the source of the materials that are used in building the plant body, he devised the following experiment. He planted a willow branch weighing 5 lbs. in 200 lbs. of dry soil. For five years he kept it watered with rain water. During this time the willow took root and grew to be a tree. At the end of the five-year period he weighed both the tree and the soil. The tree weighed 169 lbs., 3 oz., and the soil had lost only 2 oz. in weight. What possible conclusions could he have reached as to the source of the added weight of the willow? His conclusion was that water is the material from which the plant derives almost all of its entire weight. To what extent was he right? Wherein was he mistaken? In the light of your present knowledge, what else besides water ought to have been tested before drawing final conclusions?

About a century later (1727) Stephen Hales, an English clergyman, published a book "Vegetable Staticks," in which he reported an important series of experiments on which he had been at work for a considerable number of years. Most of these investigations concern parts of plant physiology not directly related to photosynthesis. The phase of his work that interests us here can be summarized in the following conclusions:

1. "Air is a constituent of living matter."
2. "Plants very probably draw through their leaves some part of their nourishment from the air."
3. "May not light also contribute much to ennobling the principles of vegetables?"

When we take into consideration that at that time no one had any knowledge of the composition of the air, and that even oxygen and carbon dioxide were badly confused in the thinking of even the most precise of the experimenters, it is remarkable that Hales was able to deduce as much as he did with regard to nutrition.

Even half a century later (1769) Charles Bonnet, a Swiss lawyer-naturalist, reporting that he had observed bubbles coming out of leaves under water but that no bubbles appeared if the water had been boiled before the experiment, was still unable to interpret his observations. We now know, as he did not, that the boiling of water drives off such dissolved gases as carbon dioxide. With this fact in mind and with the understanding of photosynthesis that he has already acquired, the student should explain the meaning of Bonnet's observations.

Only three years after Bonnet's announcement, Joseph Priestley, an English theologian-chemist, published a paper (1772) entitled "Observations on Different Kinds of Air." In his experiments he had discovered that mice in a closed vessel made the air unfit to maintain life. He also found that if plants were placed in this same air for a time, it again became safe for mice. His conclusion was that in some way plants "tend to keep the atmosphere sweet and wholesome," but animals make it "noxious." It should be clear that the mice were dying chiefly because they had largely exhausted the oxygen in the small vessel they occupied.

Spurred on by these results, Jan Ingenhousz, a Dutch physician who practiced in London, repeated and extended these experiments. He was able to report in his book, "Experiments upon Vegetables," published in 1779, that plants as well as animals "poison" the air in the dark and that plants can "improve" air only in the light. He also reported that flowers and other nongreen parts of plants "poison" air just as animals do, in both light and darkness.

Ingenhousz was so much disturbed by the danger of breathing the gases given off by plants that with a physician's concern for health he warned strongly against sleeping in a room with many house plants or living in a house closely surrounded by trees. We know now that he misinterpreted the meaning of his observations. The main point of his discoveries was that light and the green part of the plant acting together can "improve" the air.

Soon after Ingenhousz published his book the age-old riddle of the air was being solved by the combined efforts of other investigators. Instead of the erroneous idea that oxygen and carbon dioxide were simply air that behaved in a different manner under a variety of conditions, it was now discovered that these two gases are distinct from each other. They were given the names we continue to use. During the same period, progress was being made in understanding light and motion as forms of energy.

Thus the growth of knowledge in various fields of science was progressing. The pieces of the puzzle of photosynthesis were beginning to be fitted together, and the main outlines of the picture completed. The minutiae of these discoveries need not be recited here, but the degree of progress attained is shown by the writings of Dr. Julius von Sachs in Germany. In 1882 he completed his fifth edition of "The Physiology of Plants." Even a cursory reading of the English translation of this book shows a remarkable grasp of the nutrition of plants. Although the word *photosynthesis* did not come into general use until a few years later, he described the process in considerable detail.

After the publication of this book, scores of other investigators showed a great deal of resourcefulness in working out many details of photosynthesis and related phenomena. All these research workers were busy both clarifying contemporaneous understanding of obscure facts and laying foundations on which those who came later could build.

As has occurred repeatedly throughout the growth of science, progress in one field has yielded knowledge and developed techniques that have benefited other apparently unrelated subjects. Thus, coming down to our own times, the development of techniques of nuclear fission has made available ample amounts of radioactive carbon and other "labeled" elements, and it has become possible to trace the minute steps in many chemical changes which could only be surmised before 1945. Now radioactive carbon (C^{14}) can be united with oxygen, producing radioactive carbon dioxide ($C^{14}O_2$). When, under laboratory controls, this carbon dioxide is introduced into a plant under conditions suitable for bringing about photosynthesis, it is possible to trace this labeled carbon through the series of compounds into which it enters. Much of this work is still in progress, but some points are already clear.

It is known now that the oxygen given off in photosynthesis comes from the H_2O and not from CO_2; that chlorophyll so alters the energy of light that it decomposes the water into oxygen and hydrogen. The oxygen escapes and the hydrogen reacts with carbon dioxide, quickly building up carbohydrates. These steps are still under intense investigation but they are already known to be very complicated and rapid. The next discoveries must come from those whose training and experience qualify them to plan, carry out, and interpret highly technical investigations.

Fats and Proteins. The discussion thus far has treated carbohydrates as if they were the only kinds of food. This is far from the truth, because any organism will starve to death in the absence of proteins; and fats are very important or even required for the health of many living things.

Carbohydrates (sugar, starch, for example) are usually thought of as energy-supplying foods, but they are much more. They are also primary building

materials. From them either the plant or the animal may synthesize fats. It is a well-known fact that the eating of excessive amounts of sugar and starchy foods often causes people to become overweight and that feeding such grain as corn, which is very rich in starch, quickly fattens hogs and other farm animals. In like manner, the various oils and fats of nuts and other seeds as well as of some fruits, are formed in those structures from sugars that have migrated from the leaves.

Fats, like the carbohydrates, are composed of the elements carbon, hydrogen, and oxygen, but the molecule of fat contains relatively much more hydrogen and less oxygen than that of a sugar or starch.

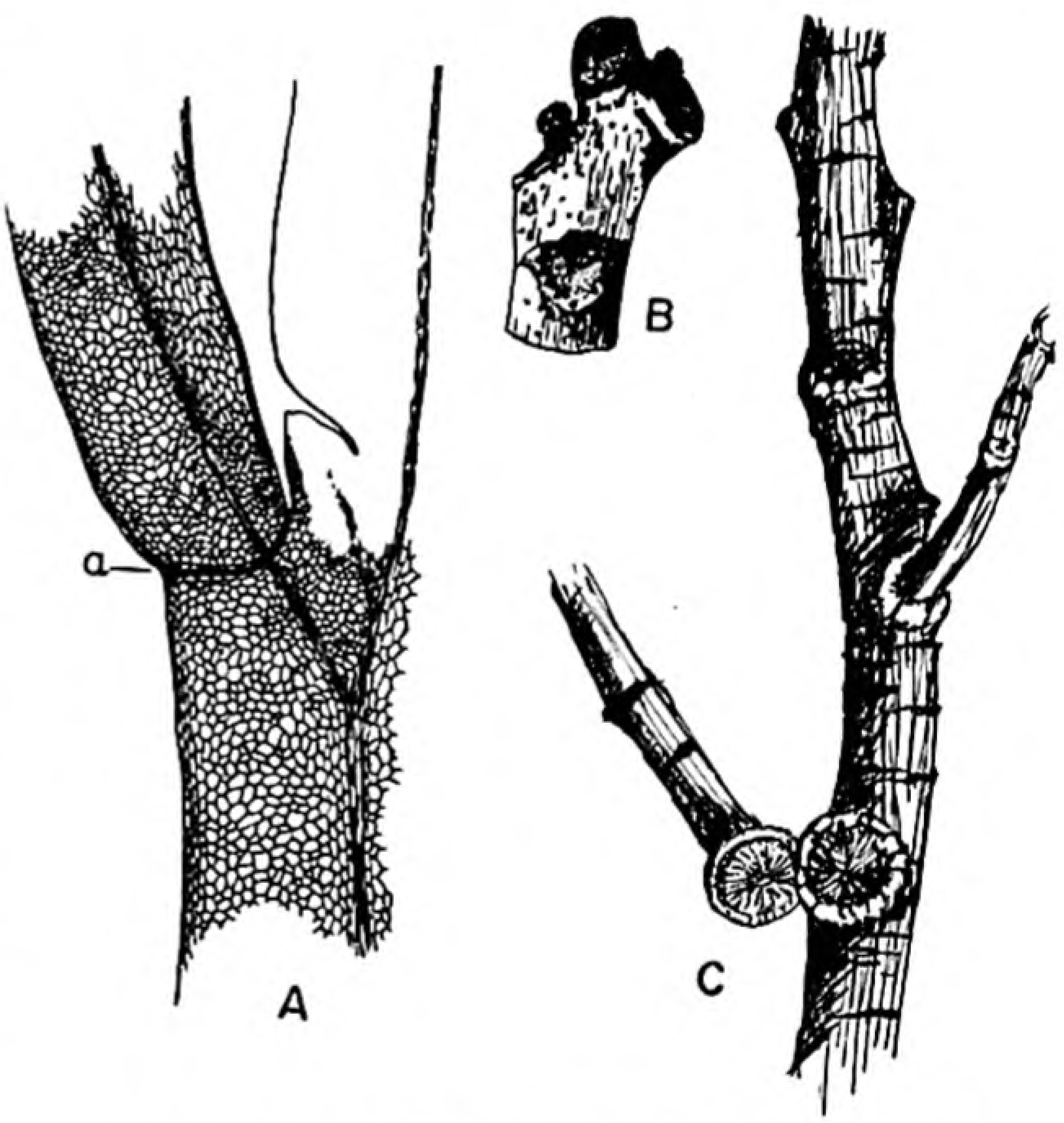
Proteins, also, are composed of the same elements as are the carbohydrates and fats, always with the addition of nitrogen, and often that of other elements such as sulfur and phosphorus. The nitrogen, sulfur, phosphorus, or other mineral substances enter the plant from the soil in the form of such compounds as nitrates, sulfates, and phosphates.

In contrast with the molecules of carbohydrates and fats, those of the various proteins are very large and complex. Chemists have not yet succeeded in determining the exact sizes and degrees of complexity of many kinds of protein molecules, but it is evident that even the simplest are hundreds of times as large as those of water and carbon dioxide.

Although proteins are far more complex than carbohydrates, and are very different from them in chemical structure, a large portion of their weight comes from materials first acquired by the plant through photosynthesis. In other words, sugars furnish much of the substance which enters into the composition of protein molecules. The energy used also comes from carbohydrates which are broken down in the process. While protein synthesis does not depend directly on light, and is, therefore, not photosynthesis, proteins could not be formed without the sugars manufactured by that process. Therefore, the supply of the various kinds of foods of both plants and animals begins with photosynthesis. If all green plants were to be destroyed, or if light should be shut off from the earth, fairly prompt starvation would be the fate of all living things.

Proteins are made largely in the leaves of plants, because wherever carbohydrates and nitrates are together in the cells, protein synthesis may take place. Under ordinary conditions of growth the largest amounts of these substances in a chemically active condition are usually found together in the leaves.

Abscission. All leaves, even those of the evergreens, eventually die and fall off. Those of perennial angiosperms of temperate climates and of climates that have annual dry seasons are usually deciduous leaves. These fall at the onset of winter



Abscission. (A) Formation of absciss layer. (a) At base of petiole. (B) Leaf scars on stem of tree-of-Heaven after abscission of leaves. Circular dots in margin of scar are leaf traces. (C) Abscission of branch from cottonwood tree.

or of the rainless season. Before they drop off, however, they undergo a considerable series of changes. Many weeks before there is any external indication of maturity, a corky layer of cells begins to organize across the base of the petiole, gradually

healing the scar which is to be made when the leaf falls. For this reason no open wounds occur when the leaves drop from the twigs.

The cells of the petiole that are just outside the cork layer gradually become detached from it. The weight of the leaf and the effects of wind or rain cause the leaf to fall off. This process is known as *abscission*, and the weak layer of cells is the *absciss layer*. The vascular bundles which extend from the petiole into the twig are never completely cut off by the absciss layer but simply break when the leaf falls. The marks which they leave, called *leaf traces*, can readily be seen in the leaf scars on the twigs of many plants during the winter.

In a few trees, such as cottonwood (see the right illustration on p. 36) and bald cypress, some of the twigs form absciss layers and fall off much after the manner of leaves.

ADVANTAGES OF ABSCISSION. Leaf fall in the autumn and renewed production of leaves the following spring probably have many advantages for those plants which follow such a cycle. But most important of all is the great reduction of transpiring, that is, evaporating, surfaces with the loss of leaves. This loss occurs at about the time when cold or frozen soils are likely to retard or completely prevent absorption of water by the roots. When these conditions of restricted absorption pass in the spring, new leaves appear and photosynthesis is resumed. Likewise, the fall of leaves at the beginning of the dry season and the resumption of growth on the return of the rainy season have the same advantages to plants living in that type of climate. A similar response to restricted supplies of water sometimes occurs in such cultivated, herbaceous plants as geraniums, petunias, beans, or coleus. These plants lose their older leaves rather soon if the soil in which they are growing becomes gradually dry.

Autumn Coloration. At the time of year when deciduous leaves are about to fall, they often display remarkably beautiful colors. While these colors delight the eye, they are actually indications of the cessation of vital activity in the leaves. Briefly, the explanation is this: Light stimulates the production of chlorophyll as long as the protoplasm in the cells remains vigorous, as during the period of growth and development (spring and summer). But light also has a destructive effect on chlorophyll. With the reduction or cessation of vital activity in the autumn the leaves gradually cease to replace the loss of chlorophyll. With the disappearance of the green chlorophyll, the color of the carotinoids is exposed, and the leaves become yellow. Most of the reds, blues, and purples seen in autumn foliage are due to a series of pigments known as *anthocyanins*. These dissolve in the cell sap and therefore contrast sharply with the colors that form in plastids. Low temperatures, an ample supply of sugars, plus the formation of the absciss layer, are among the factors, not well understood, that stimulate the production of anthocyanins in many leaves, giving the various shades of red. The combinations of green, yellow, and the colors of the various anthocyanins together with the browns of dying cells, are responsible for most of the autumn colors.

Summary. Without chlorophyll and the process of photosynthesis, life, as we know it, could not exist, because there would be neither food supplies nor oxygen for either plants or animals. Without chlorophyll we should all both starve and suffocate. Water and carbon dioxide are the substances used in photosynthesis, and the primary products are oxygen and a simple sugar. With this sugar as a beginning, the plant can reorganize the elements, carbon, hydrogen, and oxygen, forming other carbohydrates, such as starch and cellulose; or by still different processes can rearrange the atoms, producing fats; or by the addition of elements from nitrates, sulfates, and phosphates, can manufacture proteins.

The potential energy stored in all these foods comes to the plant in the form of light, which is transformed in the process of photosynthesis into the potential chemical energy required to hold the atoms of sugar together in their molecules. When other foods are formed this same energy acts to make the new molecules.

Animals are not able to carry on photosynthesis because they have no chlorophyll. Neither can they synthesize proteins from the raw materials, even

when they have access to sugars and nitrates. The green plant is the world's food-building specialist, and the leaf is the plant's most efficient photosynthetic organ.

SUPPLEMENTARY READINGS

Bonner and Galston, "Principles of Plant Physiology."
Chibnall, "Protein Metabolism in Plants."
Curtis and Clark, "An Introduction to Plant Physiology."
Frank and Loomis, "Photosynthesis in Plants."

Chapter 4

THE USES OF FOOD

Foods furnish both building materials and energy to organisms. When energy is used, food must be more or less completely destroyed; but this energy can be used either in maintaining life processes or in the building of new plant structures.

The following outline will unify the discussion of the uses of foods and summarize the succeeding pages of this chapter.

In Plants, Foods are Sources of:

1. Building Materials that are Organized into:
   a. New Protoplasm
   b. Cell Walls
   c. Reserve Foods
   d. Miscellaneous Substances
2. Energy that:
   a. Takes Part in Chemical Reactions in the Maintenance of Life
   b. Takes Part in the Formation of New Protoplasm, Walls, and Secretions
   c. Is Lost in the Form of Heat

Food and Growth. The photograph shown on p. 35 required a long exposure in the making. In fact the shutter of the camera stood open just one hundred times as long as would have been necessary to make an equally successful picture out under the open sky. When the photographer stepped from the roadway into this maple-beech forest in southwestern New York, the dense shade was bewildering for a few seconds until the eyes had become adjusted, because about 99 per cent of the daylight was screened out by the forest.

As one travels over the eastern United States he encounters extensive areas of such densely wooded land. Far overhead at the very top of the straight, slender, column-like tree trunks are the interlaced branches, supporting a canopy of leaves so closely placed that only scattered flecks of direct sunshine ever reach the ground. Inside such a forest there live thousands of diminutive maples and beech trees, only a few inches tall. They live but do not thrive. Accurate study often shows these little trees to be 10 or 15 years or sometimes even a quarter of a century old. In many cases they increase in height only a small fraction of an inch each year, because in the deep shade of the forest floor so little photosynthesis takes place that they have only a slight excess of food beyond that necessary to maintain life. Therefore very little growth can occur.

Occasionally disease causes one of the old, full-grown trees to fall, leaving an opening in the crown of the forest through which full sunshine can reach the ground. Under these conditions the starved, dwarf trees begin to grow quickly and in a remarkably short period of years their crowns become a part of the forest canopy, held on slender trunks at a height near that of the mature, fully-developed trees.

The meaning of all this becomes clear in the light of the facts discussed in Chapter 3. There it was emphasized that light is necessary to photosynthesis and that the carbohydrates manufactured in that process are required in all subsequent food-building activities. In the maple-beech forest, many of these young trees can live, but can grow little or not at all in the 1 per cent of daylight which reaches them. Growth becomes astonishingly rapid, however, when a considerable amount of sunshine penetrates to their leaves. Growth in plants as well as in animals depends in large part on the amounts of available foods present.

Food is composed of certain building materials, organized and held together as compounds by means of chemical energy. All living organisms use both the energy and the materials in their life activities. Energy is liberated from the food in the cells and much of it enters immediately into the chemical reactions involved in the formation of new compounds. Some of these may become incorporated into the structure of the protoplasm and some into that of cell walls, while still others play less conspicuous parts or are lost to the plant.

Maple-beech forest, Allegany State Park, New York. (Courtesy, New York State Museum.)

Metabolism. Three new words are now necessary to a further discussion of energy relations within living organisms. The first of these is *metabolism*, which is defined as *the total of all chemical processes in the protoplasm*. But in every chemical reaction there are energy exchanges that vary with the type of reaction. The constructive phases of metabolism, that is, those in which more complex compounds are built, constitute *anabolism* (*ana*, up) and require energy from some source outside the reaction. Such processes as photosynthesis, synthesis of fats and proteins, and, finally *assimilation* (the production of new protoplasm) are steps in anabolism. Destructive metabolism is called *catabolism* (*kata*, down). In this form of reaction, complex substances are broken down into simpler ones with the liberation of more or less energy. Catabolism is limited almost entirely to the processes of *respiration* and *digestion*.

At this point the following relationships should be made vivid:

Metabolism
- Catabolism
  - Respiration
  - Digestion

Anabolism
- Photosynthesis
- Starch Condensation
- Fat Synthesis
- Protein Synthesis
- Building of Cell Walls
- Secretion
- Assimilation

THE BUILDING BLOCKS OF PLANTS. Thus far we have assumed that all chemical compounds are constructed of atoms held together by chemical bonds and organized into molecules. This simple picture is correct and is useful in interpreting a great many facts. Organic compounds, however, go a step farther. Here relatively complex molecules, sometimes referred to as *building blocks*, become linked together into supermolecules. As an example, glucose is the usual building block of carbohydrates, and starch is sometimes called a polyglucose. The building-block character of glucose is shown clearly by two facts. When the interglucose bonds are broken in starch, as they can be both in nature and in the factory, glucose is produced. By a reverse process, glucose is condensed into starch with remarkable facility in plants.

The following discussion emphasizes only those organic compounds that are essential to an understanding of metabolism.

CARBOHYDRATES. *Glucose* is met at almost every turn in metabolism. Its formula, as we have seen, is $C_6H_{12}O_6$. *Fructose* is another simple sugar, and is especially abundant in sweet fruits. It has the same empirical formula as glucose. The distinction between the two lies in a difference in structural formulas. Both glucose and fructose are commonly called *monosaccharides*.

The most common *disaccharide* is *sucrose* ($C_{12}H_{22}O_{11}$), which is well known commercially as the highly refined cane or beet sugar. Its molecule is made up of one molecule each of glucose and fructose linked together with the loss of H_2O. Such a reaction is called *condensation*. In the plant, sucrose and then starch appear almost immediately after the beginning of photosynthesis. Some of the intervening steps are yet to be determined, but it is obvious that the condensations of sucrose and starch are both extremely complicated processes. The changes from monosaccharides to disaccharides and back again are so speedy that thus far it has been impossible to isolate the steps or to be certain whether monosaccharide or sucrose is the first product of photosynthesis.

The *polysaccharides* or polyglucoses most frequently encountered are *cellulose*, the chief constituent of cell walls; *pectin*, a cementing substance in cell walls; and *starch*, the most common storage form of carbohydrates. Cellulose and starch have the formula $(C_6H_{10}O_5)_n$. These are described as long, unbranched chains of glucose molecules linked together with the loss of H_2O at each linkage. Pectin seems to be constructed of branched glucose chains.

FATS. These substances occur in very great variety, but those that are of most apparent importance to plants are built up from glycerine, $C_3H_5(OH)_3$ and other building blocks known as *fatty acids* of which there are several. The details are not known completely but it appears that both glycerine and fatty acids are organized by the plant from sugars. The structure of glycerine is such that one molecule can react with three fatty-acid molecules. These may be all alike or of two or three kinds. Some combinations are liquid at ordinary temperatures. These are called *oils*. Examples are olive, cottonseed, and castor oil. Other fats are more or less solid at room temperature.

PROTEINS. The proteins are by far the most complex of all substances. They are constructed of *amino acids*. These in turn are derived by a complicated series of steps, only partly understood, from monosaccharides and nitrogen-bearing compounds such as nitrates and ammonium. At least 25 different amino acids are known to exist and the existence of almost as many more is suspected.

It is from the possible combinations of these building blocks with one another and with other substances that the almost endless variety of living things is derived. And the combined chemical reactions taking place among all the organic and inorganic substances in the protoplasm—all this constitutes metabolism.

RESPIRATION. Respiration may be defined as *the release of energy from food in living protoplasm*. This

energy release is usually brought about by the entrance of oxygen into chemical combination with sugars, forming new and simpler compounds, commonly carbon dioxide and water. The carbon dioxide diffuses out of the cells, while the water mingles with that from other sources.

The sugars used in respiration come from a variety of sources. They may be the unchanged products of photosynthesis, or they may be derived from starches or others of the more complex carbohydrates. When available carbohydrates are greatly reduced, any fats present may next be used, and last, proteins are drawn upon. It seems, however, that even in these cases sugars are organized from the carbon, hydrogen, and oxygen atoms of the fats and proteins before they are used in respiration.

The fact should be understood that the importance of respiration lies solely in the release of energy. Respiration must take place continuously in every active cell, or death to the cell ensues, because continuance of life requires incessant supplies of kinetic energy in the protoplasm. Under conditions of reduced activity, such as occur in dormant seeds or in plants that are inactive during the winter, the rate of respiration is greatly reduced, but even then the process probably does not completely stop. The energy set free in respiration comes to the living cells in the form of potential energy in the food and cannot be liberated except by a more or less complete breaking down of the food.

RESPIRATION AND THE RELEASE OF ENERGY. Although it is impossible to demonstrate by simple means, there is ample evidence that the energy released by respiration in a plant takes many forms and has many functions. Some of it may appear as heat and be wasted. A growing plant often has a temperature a fraction of a degree higher than the surrounding air. Release of heat is probably of no direct value to the plant, but is incidental to other processes. If the energy which appears as heat had taken some other form, it could have been used in the life activities instead of being lost by radiation. The most useful form in the plant is that of chemical energy which is used in the construction of new protoplasm from food; that is to say, in *assimilation*, which is to be discussed on p. 47.

RESPIRATION AND THE DESTRUCTION OF FOOD. Both carbon dioxide and water have weight. While water vapor and carbon dioxide gas are not obviously heavy, they can be easily weighed when condensed into liquid water and compressed into dry ice. Therefore, when sugar is destroyed in the process of respiration, and carbon dioxide and water are produced, the plant loses weight when these materials escape by diffusion. Such loss can be readily demonstrated by the following experiment: Dry seeds of known weight are planted in wet moss or other substances that can be removed from the roots when they have formed. The seedlings are allowed to grow in the dark. Why in the dark? What relation has light to the weight of a green plant? These young plants in the dark grow to be tall and slender and of much greater volume than the dry seeds from which they have developed. If these plants are kept growing in the dark for a sufficient period of time, they die. Appropriate tests show that food has been almost entirely exhausted, although the seeds from which these plants grew were originally gorged with starch, fats, and proteins.

At any time during this experiment, after the seedlings have begun to grow, they may be removed from the moss, dried, and weighed. If their weights are compared with those of the dried seeds from which they came, the seedlings are found not only to have become lighter, but the longer they have grown in the dark, the greater the loss. In some cases, when they have almost exhausted the reserve foods, the dried seedlings weigh only about half as much as the original seeds.

TYPES OF RESPIRATION. The type of respiration described above, in which free oxygen of the air unites with sugar, is called *aerobic respiration*. This is the usual type in the most actively growing parts of common green plants. Here, oxygen plays the important role of releasing all the available energy in the food. The activities involved are far less simple than the bare statement would suggest, for there are numerous steps in the process, each leading to the next, and there is evidence that various kinds of plants follow somewhat different courses. Whatever the variations, however, carbon dioxide is always given off, water is produced, and there is a high output of energy in all aerobic respiration.

A comparison of this type of respiration with photosynthesis shows the two processes to be exact opposites in their most obvious features. This statement is borne out by contrasting simplified chemical formulae of the two.

Photosynthesis

$$6CO_2 + 6H_2O + \text{Energy of light} \rightarrow C_6H_{12}O_6 + 6O_2$$

Aerobic Respiration

$$6O_2 + C_6H_{12}O_6 \rightarrow \text{Energy} + 6CO_2 + 6H_2O$$

The failure on the part of early investigators to interpret photosynthesis correctly (pp. 34–35) is easy to understand from out present vantage point. Since they had no knowledge of the existence of carbon dioxide and oxygen or of the other constituents of the air, they were unable to distinguish between photosynthesis and respiration. Even now beginning students often allow themselves to confuse these processes. Accurate understanding, however, requires that a sharp distinction be made. To this end, it is a valuable exercise to review the conclusions of Helmont, Hales, Bonnet, Priestley, and Ingenhousz, analyzing in the light of modern knowledge the true worth of their discoveries and the reasons for their mistakes in interpretation.

In contrast with aerobic respiration, in which all the potential chemical energy of simple sugars is released, under certain conditions respiration takes place without gaseous oxygen entering into the chemical changes. This type is called *anaerobic respiration* (*an-*, not; *aero-*, air; *bios*, *life*). Instead of releasing all the energy, only a small fraction of it is made available to the protoplasm. The calorie (*calor*, heat) is the standard unit of measure of energy. The large calorie, which we shall use here, is the amount of heat energy required to raise the temperature of one liter (slightly more than a quart) of water 1°C. As a means of contrasting the two types we may take the anaerobic respiration (sometimes called alcoholic fermentation) characteristic of baker's yeast. In this process glucose or other simple sugar is changed into carbon dioxide and ethyl alcohol (C_2H_5OH). If 180 grams of glucose undergo anaerobic respiration, 28 calories of energy are released. On the other hand if the same amount of glucose is changed into carbon dioxide and water in aerobic respiration, 674 calories are set free. In other words, aerobic respiration is about 24 times as efficient in supplying energy as alcoholic fermentation; and some other forms of anaerobic respiration are even less effective.

A considerable number of circumstances bring about the conditions of anaerobic respiration. If common land plants become covered with water, their oxygen supply is cut off. Nevertheless, carbon dioxide continues to escape from them for some time. In most cases, however, they soon die. In other words, they drown. During the time when carbon dioxide is being produced a small amount of energy is liberated, but only enough to maintain life for a short time. If, before death occurs, oxygen is readmitted, vigorous metabolism may be resumed, releasing larger amounts of carbon dioxide, and establishing a much more efficient energy release.

In some plant structures anaerobic respiration occurs regularly. As examples, oxygen seldom penetrates into the deep tissues of fleshy fruits or of many other large plant structures, and roots growing deep in very compact soil encounter relatively little free oxygen. And yet, all these living cell masses release sufficient energy by anaerobic means to continue their life processes.

Some of the more primitive plants such as yeasts, certain bacteria and, in fact, fungi in general, are able to live anaerobically for long periods of time. Certain species of these are unable to use free oxygen in their respiration even when it is present. An extreme case is that of a few kinds of bacteria that can remain alive but cannot grow when they are in contact with free oxygen. Some of these live only under water, in mud, or in other similar places. One that frequently occurs in soil causes the disease called tetanus or lock-jaw, which attacks man and other animals. This organism has been known to live for many years in ordinary soil in an inactive resistant "spore" stage. If some of this infected soil is driven deep into a wound where the free oxygen of the air is excluded, vigorous growth may occur, resulting in the disease. One important reason for the common practice of keep-

ing deep wounds open and of using cotton or other loose materials for dressings is that air is admitted, thus suppressing the growth of anaerobic bacteria such as those that cause tetanus.

Many plants respire aerobically whenever oxygen is available and anaerobically when it is deficient. Water plants such as cattails, water lilies, and bulrushes have extensive systems of loose, open tissues through which air diffuses freely. In many of these plants the intercellular spaces extend as uninterrupted passageways from the leaves to the roots. During photosynthesis the oxygen that is given off diffuses in great quantities through the spaces, richly supplying all the tissues of the plant. Under these conditions aerobic respiration progresses with great vigor. When night comes and photosynthesis ceases, the remaining oxygen becomes rapidly depleted and anaerobic respiration gradually replaces the aerobic form.

Digestion. A dry kernel of wheat contains a high percentage of starch and smaller amounts of fats and proteins but, normally, no sugar. If the wheat begins to grow, however, chemical tests within a few days can prove that it has become richly supplied with sugar while at the same time microscopic examination shows that the grains of starch are disintegrating. The starch is being changed into sugar—is being digested.

Digestion may be defined as *the process of changing insoluble foods into forms which are soluble and capable*

Digestion of wheat starch during germination.

of passing through colloidal membranes. In the example above, the insoluble starch becomes sugar, which goes into solution in water and diffuses readily through the colloidal cell structures. In the growing seedlings this sugar is transferred into the young, enlarging root and shoot where a part of it is decomposed in the processes of respiration and other parts become building materials in the construction of the new developing tissues.

Not only in seeds, but in any plant part, wherever starch is located, it must be changed to sugar by a process of digestion before it can be used in metabolism. Likewise, foods in the form of fats and proteins must also be digested, for neither of them is soluble in water. The final digestion products of starches, celluloses, and other carbohydrates are various sugars; those of proteins are amino acids; and those of fats are fatty acids and glycerol—the latter is known commercially as glycerin. Thus digestion results from the separation of the foods into their constituent building blocks. In the case of fats, however, there is evidence that, once formed in a cell, they cannot leave in the form of glycerol and fatty acids but are sometimes changed back to sugars; in which case they can migrate or be used in metabolism. Digestion, then, changes foods into useable forms.

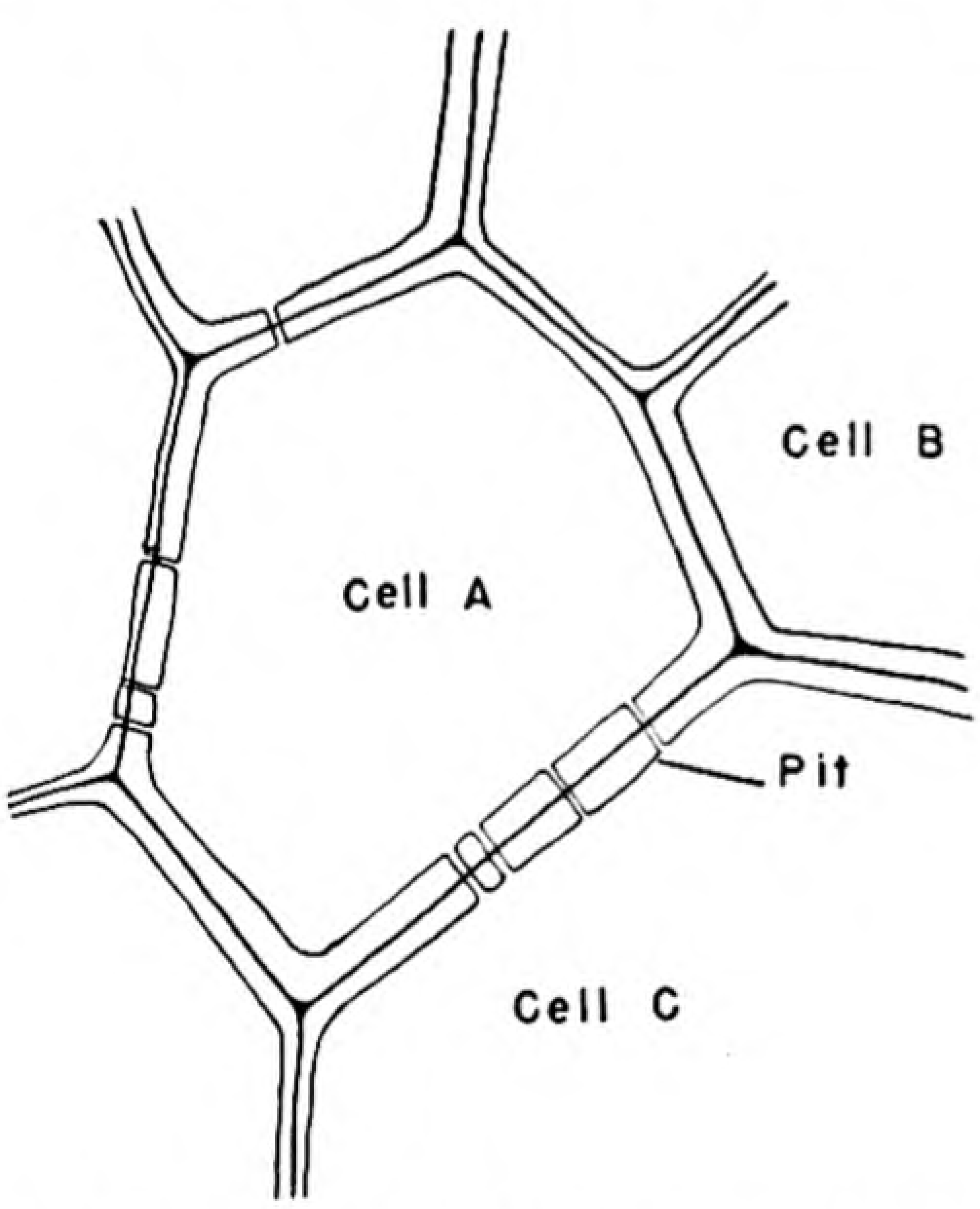
Catabolism, including respiration and digestion, as has been said earlier, is a term that can be applied to any form of metabolism in which complex substances are reduced to simpler forms. It is now a familiar fact that in respiration foods are broken down in such a way that they release their energy. In digestion, on the other hand, the foods are reorganized into forms that dissolve readily but the energy release is not significant.

Anabolism. A young, growing robin in the nest is said to eat more than half its own weight in food every day. This food is quickly digested and a part of it is broken down in the process of respiration, furnishing the various types of energy the nestling requires in its life processes. The remainder is built into the complicated protoplasm of the rapidly growing bird. The dead products of digestion are becoming living muscle, nerve, and connective tissue.

The birdling's food is brought to it by its parents. The young plant, in contrast, must produce its own from materials that are not food, but in both cases the results are similar. Foods are built into the tissues of the developing organisms, and growth results.

The various phases of food synthesis by plants have been discussed in Chapter 3. Because they are constructive processes, photosynthesis and the synthesis of fats and proteins are all to be classified under the general heading of anabolism. But the manufacture of foods is only an initial part of the series of activities by which a great variety of more complicated substances comes into being. As yet, no one knows just how many of these products there may be; nor are the details of the anabolic steps involved in constructing them understood.

THE BUILDING OF CELL WALLS. Cell walls of plants are, with rare exceptions, constructed of materials that are either carbohydrates or are derived from them. Cellulose, one of the commonest of all components of cell walls, is a carbohydrate closely related to starch. *Lignin*, the characteristic constituent of wood; *cutin*, a water-proof mixture that frequently forms a coating called the *cuticle* on the outer surface of leaves and young stems; *suberin*,



Cell walls. The dark line between adjacent cell walls is the middle lamella. The protoplasm of cells A, B, and C has built the walls as indicated.

the material that characterizes cork; and a considerable number of waxes, resins, and gums, all are derivatives from carbohydrates.

Still another of these substances related chemically to starch and cellulose is the jellylike *pectin*, which commonly acts as a *middle lamella*, or layer of cementing material, between the walls of adjacent cells, somewhat after the manner of mortar between the bricks of a building. It should be explained here that each individual protoplast surrounds itself with its own wall and that what seems to be a single wall between two adjacent cells is actually made up of three layers, the walls of the two cells and the middle lamella between them.

This type of construction results from the following sequence of events:

At the time when a cell divides, producing two new ones, in the usual type of plant tissue (p. 14) plasma membranes organize, separating the two daughter protoplasts. The details of this action are obscure but pectin appears quickly between these cell membranes. This separating layer between two very young cells is often called the *cell plate*. The pectic portion becomes the *middle lamella* mentioned above. On its surface each of the new cells begins promptly to deposit a *primary wall*, made up of a mixture of cellulose and pectin. It will be recalled (p. 41) that pectin and cellulose are both polyglucoses, but the glucose molecules are attached to one another in different arrangements. In both the middle lamella and primary wall there is considerable intermixture of these two carbohydrates. Such walls are very flexible and extensible, permitting considerable change in form and size of the enclosed cell.

In elongating structures, such as growing stems or roots, the new walls are especially extensible in the direction of maximum growth, but much less so in other directions. Relatively little detail in structure of these young walls can be seen with the microscope, but studies with the X-ray and the electron microscope are revealing a great deal. The glucose molecules in cellulose are held together as building blocks by chemical bonds. These cellulose particles are organized in the form of *fibrils*, which in turn are woven together into a sort of network. During cell elongation this fabric becomes loosened, but other strands are woven into the opened texture. After a time *secondary walls* may be added in the form of two or three layers of cellulose fibrils applied to the inner surface of the primary wall and extending parallel to

each other either in straight or in spiral patterns along the length of the cell. In wood and other mechanical tissues, *lignin*, a firm, waxy substance mentioned above, becomes infiltrated into the spaces within the fibrillar network of cellulose, giving the characteristic hard texture of such structures. Lignin may occur in any layer of the cell wall from the middle lamella out. Though it hardens these woody walls, it in no way adds tensile strength to them. Instead, the cellulose, which may constitute about three-fourths of the material, furnishes almost all the strength. With the completion of the secondary walls, all enlargement of the cell ceases.

For some reason not yet understood, secondary thickening does not take place uniformly all over the cell wall. Therefore there are usually thin places or even minute canals through the walls, apparently allowing the plasma membranes of adjoining cells to make contact, if not perhaps to merge. These thin places through the walls are called *pits*. Sometimes they are very definite in position and form. At other times they are rather vague. The minute protoplasmic connections between adjoining cells are *plasmodesmata* (singular, *plasmodesma*). There are several unproved theories to account for their presence: that they are channels of transfer of materials between adjacent cells; that nervelike impulses travel from cell to cell in this way; and that they are only relicts of protoplasm which were not quite severed when the wall formed. In any case, their presence should be recognized and their function left to future investigation. When the cells have become mature the pectin commonly unites, chemically, with calcium to form calcium pectate, a compound which is strong enough to cement the walls firmly together.

THE PRODUCTION OF SECRETIONS. Hundreds of substances of almost endless variety are organized within the protoplasm of various kinds of plants. These may be classed properly as *secretions* produced by the cells. And since they are almost all built up from simpler substances, their production should be classified as a part of anabolism. Some of these are responsible for the flavors and odors characteristic of certain plants. A few are extracted and used as commercial products, such as camphor, oil of citronella, menthol, and quinine. Others that are well known are the peculiar flavors of apples, bananas, onions, and mustards, to mention only a few.

Others of these secretions by the cells of plants are a considerable number of pigments, including those most important constituents of chloroplasts, the two chlorophylls and their constant associates, the carotinoids. In addition, the various blues, reds, and purples are usually produced by *anthocyanins* of many kinds. These dissolve in the cell sap and can, therefore, be found chiefly in the vacuoles. They vary in color with the different degrees of acidity of the cell sap and also with the presence or absence of small amounts of such minerals as iron and aluminum. The almost endless possible combinations of colors resulting from these variations, plus those from the different concentrations of the carotinoids and their chemical allies ranging from clear yellow to brown, together with the larger or smaller amounts of chlorophyll, are responsible for almost the entire range of colors found in common plants. Aside from the chlorophylls, there is still much question as to the importance of these various secreted pigments. Some of them will probably be found, eventually, to play important parts in metabolism, while others may be only incidental by-products of some of the reactions taking place within the cells.

While the direct importance of certain of these secretions may be open to question it is known that in many cases the colors and odors of flowers attract insects to them, bringing about the transfer of pollen and the resulting production of seeds. This is not a clear-cut function in the same sense that chlorophyll has the function of carrying on photosynthesis, but colors and odors are necessary directive agents in the transfer of pollen in some species of plants.

Investigation shows that insects do not distinguish the refinements of color and odor resulting from slight chemical differences within these plants, but some of them are definitely attracted or repelled by certain flowers. As an example, in an open grove in the Middle West, where oak and hickory trees stand far apart and shrubs and smaller

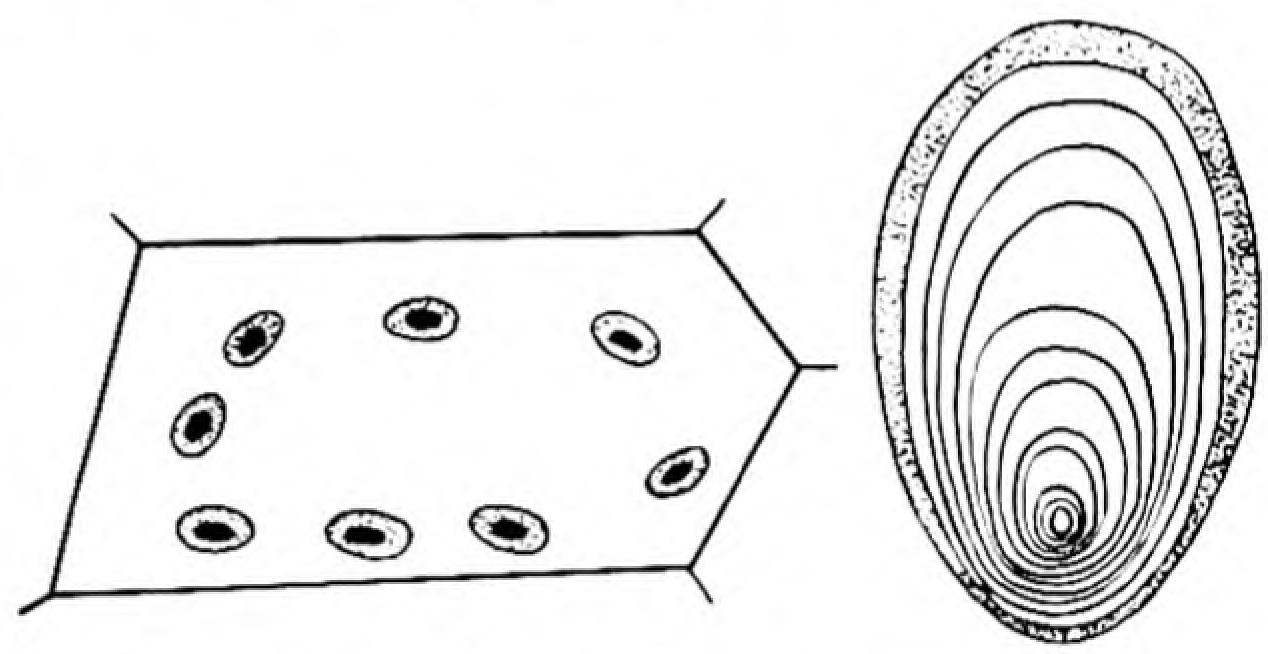
plants cover the ground, the hawthorns and wild crab apples blossom at the same time in spring. Then, honeybees and flies abound on any sunny day. For many years, botany classes tabulated the results of their observations of insect reactions to flowers in such a grove, always with the same report. Even when the hawthorns and crab apples were growing side by side, the flies visited the former and the bees the latter, both in great numbers, but practically never was a fly found to alight on a crab apple flower or a bee on a hawthorn.

These small trees are of about the same size and their flower clusters are much alike. The crab apple blossoms have a pinkish color while the hawthorns are almost white. The greatest difference observable to a human being is that of flower odor, which is very pleasant in the crab apple and mildly offensive in the hawthorn. But for all their similarities, the insects are not confused, and the pollen is distributed in an efficient manner, being restricted to flowers of plants within the same species.

Other secretions, to be discussed presently, are the enzymes, auxins, and vitamins, which play various necessary parts in metabolism, bringing about the chemical changes involved in respiration, digestion, and growth. In fact, without these it is doubtful if life processes could continue. Therefore, these substances make protoplasm possible, but are themselves the products of protoplasm.

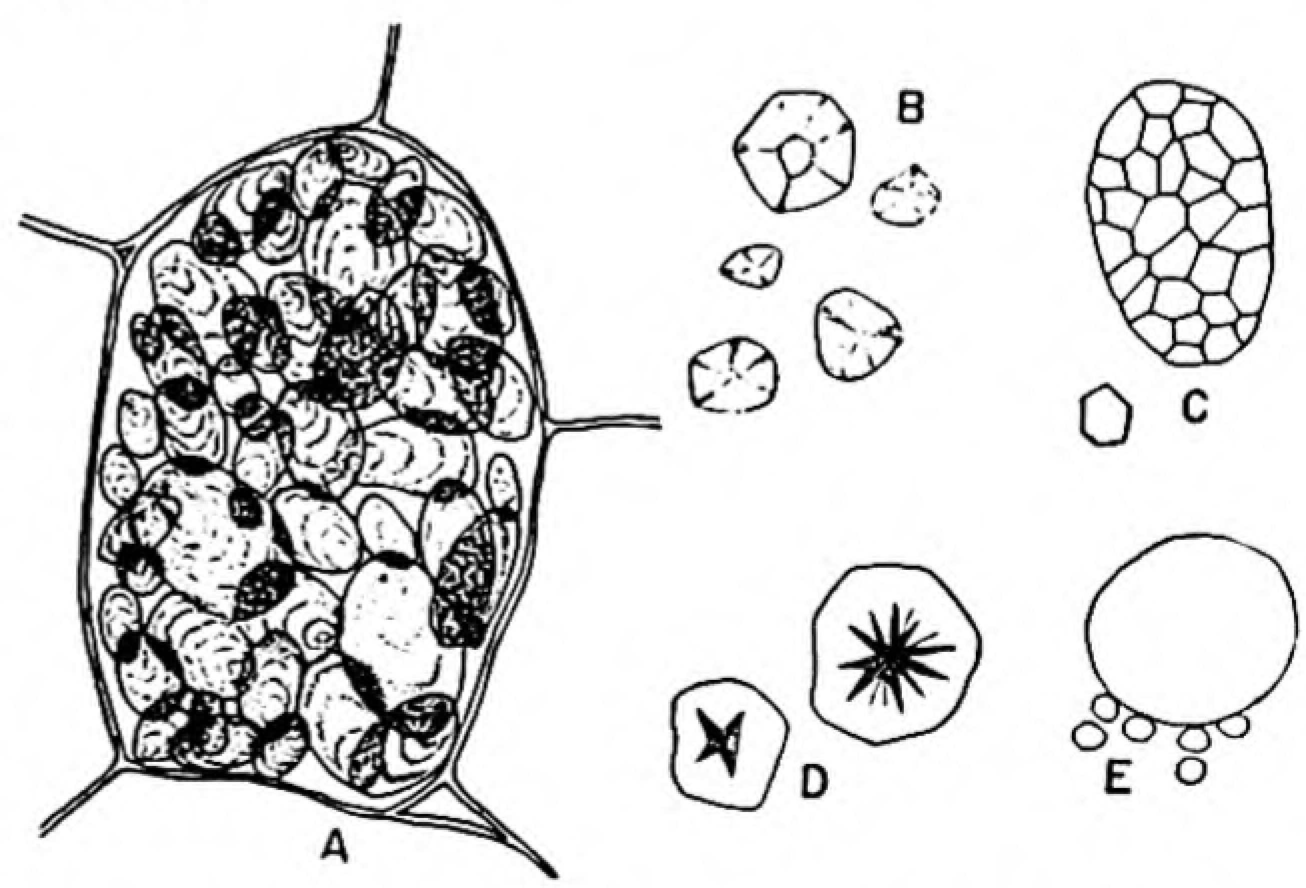
ASSIMILATION. The most complicated of all phases of anabolism is assimilation, that process or set of processes by which new protoplasm is built. Assimilation may be defined as *the changing of non-living materials into living protoplasm.* Fragmentary steps in the organization of various types of foods are rather well understood and in some cases can be more or less completely repeated in the laboratory. But no one knows just what happens when non-living nutrients take on that characteristic called life. It is only known, as yet, that in some way foods are reorganized by the protoplasm and are built into its own structure. If the material added replaces molecules or parts of molecules that have been lost as a result of catabolism, assimilation amounts to repair; but if the new protoplasm is added to that already present, it becomes growth. Growth depends ultimately on assimilation, because neither the number of cells nor the size of the plant can increase indefinitely without increased amounts of protoplasm.

Reserve Foods. As soon as the rate of manufacture of foods exceeds that of use in metabolism, the food excess accumulates in certain cells of the plant. In some plants storage occurs in such quantities as to enlarge greatly the parts in which it



Development of starch grains. (*Left*) Small grains forming in chloroplasts. (*Right*) A large grain inside a leucoplast which is stretched to a thin layer around the starch.

accumulates. In swollen storage organs the cells increase in size and number as they gradually become gorged. In most plants, however, large amounts of food accumulate in the ordinary cells, especially those of roots, stems, fruits, and seeds. Any living cell, with the exception of a few highly specialized ones, may become a respository for foods.



Starch grains. (A) Potato starch grains surrounded by cell walls. (B) Grains of corn starch. (C) Compound grain of oat starch. (D) Starch from bean. (E) Wheat starch.

Carbohydrate reserves usually take the form of starch, although sometimes they remain as sugars, as in the case of most fruits, sorghum cane, sugar cane, and sugar beets. Sugar, when present, dissolves in cell sap. Starch, on the other hand, is not soluble in water, but takes the form of grains within the cells. Leucoplasts and chloroplasts form the centers in which the starch grains develop. Starch grains of the various species of plants are so different in appearance that it is often easy to distinguish those from different sources.

Fats and oils are frequent storage forms, especially in certain seeds. The chief difference between these two substances is that fats are solid at usual temperatures and oils are liquid. This form of food storage is especially pronounced in various nuts, where fats frequently constitute more than 50 per cent of the weight. Although nuts, as a class, contain large quantities of fats and oils, almost all seeds have some food in this form. Olives, castor beans, and cottonseed, as is well known, store large amounts of oils.

Stored protein is found chiefly in seeds and fruits. Peas, beans, peanuts, some strains of corn, and the outer layers of wheat grains are especially rich in proteins.

Enzymes. If it were possible to see the interplay of action among the atoms in living, growing protoplasm—the intake and outgo of energy as certain substances break down, freeing energy which forthwith attaches itself elsewhere only to draw in still other atoms—it would be easier to understand the immensely intricate processes by which matter and energy act and react upon each other, tearing down and rebuilding in that whirlpool of life activity called metabolism.

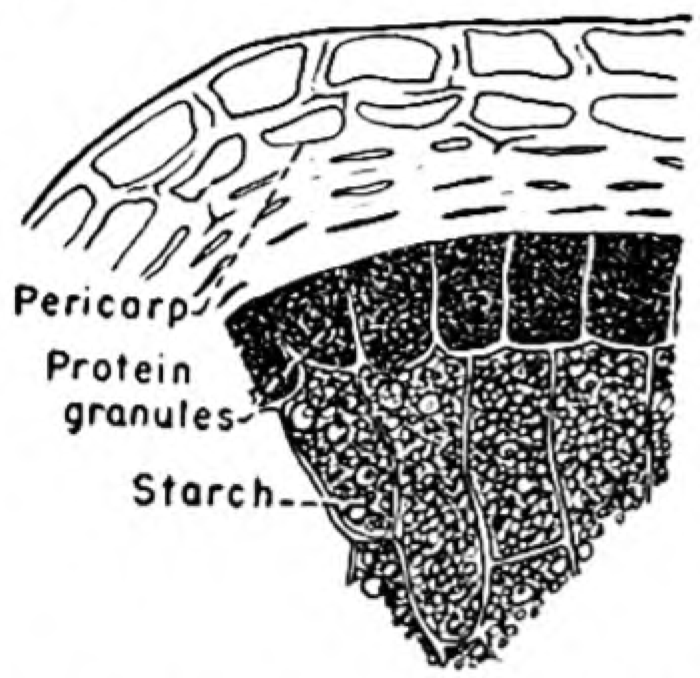
These activities are brought about by means of certain products of protoplasm called *enzymes*. The word enzyme (Greek *en*, in; *zymē*, leaven or yeast) was coined by the German physiologist, Wilhelm Kühne, who reported in 1878 the discovery of some unidentified substance in yeast which was responsible for the well-known fermentation of sugar with the formation of carbon dioxide and alcohol. This discovery precipitated a controversy. Some scientists were convinced that the yeast cell itself brought about these changes by its own activity. Others thought that the agent was secreted by the yeast plant. Then as now, the solution of such a problem could be attained only by the most exacting experimentation. It was almost twenty years before investigators were able to overcome various faults of technique. The final step in resolving this disagreement came when Edward Buchner succeeded in collecting a liquid by grinding living yeast and removing the broken fragments with a filter. He found that this cell-free filtrate brought about rapid fermentation of sugar. Thus he proved that the enzyme was actually derived from the interior of the cells and that the living cells themselves are not necessary to the action. This investigation established the fact that the enzymes are secretions produced by the living cells.

It was evident that the fermentation of sugar was somewhat similar to the well-known action of the digestive juices in the alimentary canal of an animal. Therefore the name enzyme soon came to be applied to each of the active principles of these secretions as they were isolated. Physiologists, both plant and animal, gradually discovered that not merely a few but a very great number of phases of metabolism are brought about by the action of enzymes, each carrying out its one single step.

Many of these processes can be accomplished by usual chemical means with the use of heat and concentrate solutions. Either of these, however, would kill the cells. The enzymes are remarkable because they catalyze reactions at temperatures and under other conditions that are entirely safe for living protoplasm. As an example of this contrast, starch can be changed to sugar in a test tube if it is heated with an acid. On the other hand, the enzyme diastase brings about this reaction many times more rapidly, at low temperatures, and without harm to the cells in which the transformation takes place. The extreme efficiency of an enzyme can be illustrated further by the fact that a measured amount has been shown to transform a million times as much substrate as its own weight.

By way of summary we may present the following definition: *An enzyme is an organic catalyst pro-*

duced in the living cell, capable of bringing about a chemical change which otherwise cannot be made in the protoplasm, or which would take place too slowly to be effective in life processes.



Section cut through the outer part of a wheat grain.

THE KINDS OF ENZYMES. Two types of enzymes, *respiratory* and *digestive*, are generally recognized and a third, *anabolic*, which may prove to be a large group, is definitely known only in the case of the chlorophylls.

The most successful studies of this group of substances have been done with the digestive enzymes. These bring about changes known as *hydrolysis*, (*hudor*, water; *lysis*, solution). This means that in producing simpler, more readily soluble compounds, water enters into the reaction. The steps in the digestion of starch by common plants will illustrate and clarify this statement.

$$\underset{\text{Starch}}{2(C_6H_{10}O_5)n} + \underset{\substack{\text{In presence}\\\text{of diastase,}\\\text{an enzyme}}}{n\,H_2O} \rightarrow \underset{\text{Maltose, a sugar}}{n\,C_{12}H_{22}O_{11}}$$

This formula may be interpreted by saying that "n" is an unknown number because the exact degree of complexity of starch has not been determined, although the relative number of atoms of carbon, hydrogen, and oxygen are well known. Under the influence of diastase, water enters into chemical combination with starch, yielding a soluble sugar, maltose. But maltose is not a final product of digestion. It may be acted upon by maltase, producing a still simpler sugar, glucose, as follows:

$$\underset{\text{Maltose}}{C_{12}H_{22}O_{11}} + \underset{\substack{\text{Water in}\\\text{presence of}\\\text{maltase}}}{H_2O} \rightarrow \underset{\text{Glucose}}{2C_6H_{12}O_6}$$

In this case, the more complex molecule of maltose is changed into two simpler ones of glucose by the introduction of a molecule of water. Thus, by two steps of hydrolysis, insoluble starch has been transformed into glucose ready to be used in metabolism or to be transferred to other parts of the plant. While the numerous types of hydrolysis in the different foods vary considerably from one another the general digestive action is fundamentally similar in all. In all cases the food is reduced to its constituent building blocks.

Individual enzymes of all types are commonly named according to the kind of materials on which they act. A group of these, called *carbohydrases*, hydrolyze the various carbohydrates, each of the numerous types of carbohydrates being acted upon by a definite enzyme. Likewise, *proteases* digest proteins, *lipases* change the lipins or fats, and *oxidases* control the actions of oxygen.

The following outline should organize the preceding statements and make them more readily understood:

- Hydrolytic Enzymes
  - Lipases
  - Carbohydrases
    - Diastases
    - Cellulase
    - Maltase
    - Sucrase
    - Pectinase
  - Proteases
    - Pepsins
    - Peptidases
- Oxidizing Enzymes
- Anabolic Enzymes

Hydrolytic Enzymes. All of these bring about digestive action.

Lipases. This is a general name applied to a group of enzymes that change the various types of fats into their constituent fatty acids and glycerol.

Carbohydrases. This is another large group of enzymes each of which brings about the digestion of some one type of carbohydrate. For example, evidence indicates that there are probably several of the *diastases*. They change starch to various kinds of dextrin and then to maltose. *Cellulase* is an en-

zyme that digests cellulose, producing glucose. It is found in a wide variety of plants. Sometimes it is present in germinating seeds and it is frequently secreted by wood-decaying fungi and bacteria, where it brings about the change of the cellulose of the wood into glucose. This is readily absorbed and used by the fungi that produce the secretion. *Maltase* changes a complex sugar, maltose, to glucose. It usually occurs as an associate of the diastases and carries to completion the digestive action which they begin.

Proteases. This is another huge group of enzymes that digest proteins and their products. The *pepsins* appear to be a large group of enzymes that act on proteins. They are found in both plants and animals, although they may not be identical in various organisms. The characteristic that marks all of them is that they can change the proteins, which are excessively complex, to simpler products, called polypeptides. *Peptidases* further digest the polypetides, breaking them down into the various amino acids, of which there are at least twenty-three kinds. These are all soluble in water and are capable of diffusing through the colloidal membranes of living cells.

Oxidizing Enzymes. These have respiratory functions. There appears to be an extremely large number but they are so poorly known that they cannot, as yet, be named, although they are often given the general name of *oxidases.* So far as is known their chief action brings about the union of oxygen with foods, releasing energy in respiration.

Anabolic Enzymes. Chlorophyll *a* and chlorophyll *b* are the only enzymes known definitely to carry on a constructive process but there is a considerable amount of evidence that other anabolic enzymes exist which bring about many or perhaps all such changes.

At this point it should be understood that the plant has no special organs in which the various enzymes act. Instead, in any cell there may be a considerable number of enzymes, each ready to carry on its own limited activity when conditions become right. As an example, a cell containing starch grains may also have, within its walls, diastase, maltase, and oxidases. When temperature, moisture supplies, and other necessary factors in the environment become suitable, the diastases carry the starch through a series of steps ending with the production of maltose. When this sugar begins to appear in the cell sap the maltase digests it to glucose, which in turn may be broken down by an oxidase forming carbon dioxide and water in aerobic respiration. This is, perhaps, one of the simplest series of steps one could choose to represent the chainlike sequence of events carried on by a battery of enzymes, but such series appear to be almost universal. Each action depends on the one before it, step by step back to the very beginning, and without that initial enzyme none of the others could function. Thus, in the illustration, without the diastases acting on starch, aerobic respiration could not have taken place.

Vitamins. At the present time we are in the midst of a remarkable period of advance in our understanding of the chemistry of life processes. The combined efforts of animal physiologists, plant physiologists, and biochemists are producing a clearer picture of both the structure and the functioning of enzymes. Some are obviously true proteins but others are now shown to be of dual nature. In these latter the main body of the enzyme is a protein particle to which is attached a so-called *prosthetic group* (Greek *prosthesis*, an addition) which may or may not be another protein. For the enzyme to function, both parts must be present. Any condition which removes or inactivates either segment prevents the functioning of the enzyme.

It is now becoming evident that the vitamins are either prosthetic groups themselves or are necessary parts of these groups. We have seen that there are very great numbers of kinds of protein. Several prosthetic groups have already been discovered. Among these are some of the *trace elements* such as copper and zinc. (p. 93) Each prosthetic group is capable of acting with any of a large number of proteins to form an enzyme. In other words, of the hundreds of enzymes known to function continuously in protoplasm, many or all are different combinations of proteins associated with the various prosthetic groups. Each combination appears to carry out a slightly different function from the rest. With these facts before us it becomes evident that the

lack of a vitamin results in the failure of one or several steps in metabolism. The symptoms of vitamin deficiency so well known to the animal physiologist are then the obvious abnormalities caused by faulty or incomplete functioning of the protoplasm. Thus a deficiency in vitamin D, calciferol, causes impaired calcium metabolism. Common human symptoms of vitamin-D deficiency are such physical deformities in childhood as improper development of teeth and a failure of bones to harden normally.

For many years the only means of studying the vitamins or even of discovering their existence was by controlled experimentation with the diet of animals. Now, some of these substances are so well known that they are produced commercially by purely chemical means. When vitamins were first being discovered, each was named by a letter of the alphabet, as vitamin A, vitamin B, vitamin C. Investigations continued, however, and some were shown to be not a single substance but several. This statement applies especially to vitamin B, which has now been separated into about a dozen segments and is often called the vitamin-B complex. As the various vitamins have come to be understood chemically and physiologically, each has been given a more precise name.

Recently investigators have developed a remarkably ingenious method of studying the effects of the various vitamins on metabolism. Most common plants are now known to produce adequate amounts of all vitamins for their own needs, while many animals are dependent upon plants for their supplies. Because green plants in the light are usually independent of outside sources, they cannot be used as test subjects as can laboratory animals. The plant physiologist has discovered three important tools with which to work. First, the roots of many plants are dependent on the growing leafy shoots for their supplies. Accordingly, root tips are removed and kept alive in the dark under aseptic conditions. These root tips are placed in solutions containing sugar and all necessary inorganic minerals. Then measured amounts of the vitamin being investigated are added. By comparing growth rates, respiration, and other physiological functions, the effects of the vitamin are determined with great precision. Second, embryos are removed from seeds and studied in the same manner as roots. Third, a few strains of yeasts and molds have been discovered which cannot produce certain of the vitamins. These also are extremely valuable subjects for the critical study of the vitamins. Such highly precise techniques in the hands of numerous investigators using animal as well as plant tissues, have led to the conclusion that all protoplasm requires a considerable assortment of vitamins.

These exacting studies have revealed that almost unbelievably low concentrations of vitamins are sufficient to bring about normal activity in the protoplasm. Thus the addition of biotin (See p. 52) at the rate of 1 part in 50 billion parts of culture medium resulted in twice as much growth of a yeast culture as occurred in the control. This is an extreme case, but other vitamins are found to be adequate for normal metabolism in concentrations that are expressed in terms of parts per million.

The exact role played by each vitamin in the life of a plant is understood only in part. Since many animals (and especially man) produce some of the vitamins only feebly or not at all, it becomes evident that plants constitute the only sure source in nature. Here once again the plant holds a key position in the world of life.

The table on p. 52 is a summary of present knowledge of sources and functions of the well-known vitamins.

Growth Substances. Not only are there large numbers of enzymes, each with its own effects on metabolism, but within recent years another type of plant product has been discovered. This kind of secretion goes by the various names of *auxin*, *hormone*, and *growth substance*. The auxins are recognized by their effects on growth, hence the name which comes from a Greek word meaning "to grow or increase." The word hormone means "a messenger," referring to the fact that at least some of these secretions travel from one place to another, bringing about their peculiar effects wherever they go. At least three complex growth substances have been identified in plants and are known to be common in parts which are actively growing. They are

called auxin *a*, auxin *b*, and heteroauxin. Heteroauxin is now commonly called indoleacetic acid, or IAA. Some simpler compounds, such as ethylene gas (C_2H_4), occur in ripening fruits and are definitely known to take some part in maturing processes. Opening buds, apical meristems of germinating seedlings, flower stalks, and immature leaves are especially richly supplied with various auxin-like materials.

Name	*Source*	*Physiological Functions*
Vitamin A	Carotinoids in plant changed into vitamin A in animal.	Unknown in plants
Vitamin B complex		
*Thiamine (Vitamin B_1)	Mature leaves. Carried to roots and young developing leaves and seeds, where it becomes highly concentrated. Also produced by many fungi and bacteria. Synthesized commercially.	Respiratory function. Necessary for cell division and growth of root and embryo; carbohydrate metabolism; not stored; must be supplied continually.
*Riboflavin (Vitamin B_2)	Follows same pattern of formation and distribution as thiamine. Synthesized by almost all plants.	Respiratory function; one of several enzymes involved in respiration.
*Pyridoxine (Vitamin B_6)	Green leaves. Transferred to all parts of plant. Synthesized commercially.	Prosthetic group in enzyme system forming amino acids; protein metabolism; root growth; necessary to all organisms.
*Niacin (Nicotinic acid)	Green leaves in light.	Actions closely integrated with those of pyridoxine. Plays parts in protein and carbohydrate metabolism and respiration; necessary for root growth in at least some plants.
Pantothenic acid	Not determined in higher plants, but widely distributed. Synthesized commercially and by some bacteria.	Necessary for root and embryo growth; also for yeast and other microörganisms.
Biotin (Vitamin H)	Not determined, but found in all plant and animal tissues. Synthesized commercially and by bacteria.	Part of respiratory enzyme system; affects vigor and growth in embryo.
Ascorbic acid (Vitamin C)	Dogs and rats synthesize their own; man does not. Highly concentrated in leaves and meristems, especially just before flowering. Synthesized commercially.	Seems to be necessary for plant growth. Plays part in respiration. May be important in the flowering of higher plants.
Calciferol (Vitamin D_2)	Fats in ultraviolet light. Synthesized by almost all plants.	Calcium metabolism in animals.

* Hormonal in action.

Experiments indicate that, when in the light, the growing leafy tips of shoots are largely responsible for the production of growth substances. From these sources the hormones travel to all parts of the plant, controlling in a variety of ways the development of various parts.

For reasons which are not yet fully understood, the same auxins that cause growth of young leaves may also prevent axillary buds from developing into branches. This fact explains the formation of lateral branches just behind the terminal bud after the growing tip of a stem has been removed, because, with the loss of the terminal region, the source of the auxins that inhibit the growth of lateral buds is removed and they begin to develop into branches. The contradictory actions of these hormones are further emphasized by the fact that they stimulate the production of branches on roots and of adventitious roots on stems, while at the same time retarding the elongation of these roots when they are once formed. Experimental evidence is accumulating to show that these differences in growth behavior in various plant organs result from

corresponding peculiarities in the protoplasm of different parts of the plant. In some species, at least, an amount of growth substance sufficient to stimulate active development of a leafy shoot will inhibit root growth, but if the auxin is sufficiently diluted, root formation and elongation may occur freely on condition that another secretion, vitamin B_1 (thiamine), is present.

The chemical structure of auxin *a*, auxin *b* and heteroauxin has been determined and these growth substances can now be manufactured for both experimental and commercial use.

Besides these growth-regulating substances that are known to be formed in the tissues of plants, dozens of other materials have been discovered that bring about similar results. By the proper use of some of these compounds that can be produced by the manufacturing chemist, it is possible to root cuttings more quickly than ever before. They are applied in dilute solution in water, as very small amounts in salve-like mixtures with lanolin, or sometimes as dusts with talcum or other powders. By such means it is even possible to propagate a considerable number of trees and shrubs which previously could hardly be brought to produce adventitious roots. Among these are such important trees as pear, chestnut, and various pines and maples. In this way the secretions of plants are being supplemented by the products of the laboratory.

Roots forming on stem of tomato plant as a result of application of a small amount of growth substance a few days before photograph was taken.

Something in the nature of an auxin is now being shown to affect the development of flowers and fruits. If certain substances, as yet known only by their effects, are transferred from a plant that is in flower into other plants that are purely vegetative, the latter begin at once to organize flower buds. Likewise pollen extracts or some of the auxins, when injected into the ovaries of certain flowers, cause them to develop into seedless fruits, even without normal fertilization taking place. New information is coming so rapidly from those who are actively engaged in research in the field of growth and development, that one cannot speak with the assurance that statements made will not require emendation or supplementation within a brief space of time. But these studies are so fraught with possibilities of many kinds that even the elementary student should be aware of them.

Reference to the table on p. 52 makes it clear that at least a few of the members of the vitamin-B complex are produced in apical regions of the growing shoot and function in the growth of roots, stems, fruits, and embryos. Since these

vitamins are concerned with growth they are properly classed as auxins as well; and since they must travel from the point of origin before they complete their functions they are also hormones by definition. In other words, these secretions enter into so much of the metabolism of the plant that a single designation is not adequate to delimit them. The tendency now is to class *all secretions that function in trace amounts at points distant from their origin as hormones.*

In an earlier paragraph, p. 52, mention was made of indoleacetic acid as one of the growth substances. This and a few chemically related compounds are now gradually coming into general use in agricultural and horticultural practice. These substances, with others that supplement their action, are supplied in trace amounts in the form of spray or dusts. Some of these treatments are used to promote flowering in certain plants. Others reduce the number of fruits produced, with correspondingly larger and finer quality for those few. Still others prevent preharvest drop of such fruits as apple, apricot, peach, and pear.

Another widely expanding field of usefulness of synthetic hormonelike substances is the control of weeds. DDT and related compounds, greatly diluted with water and sprayed over weeds, bring about the destruction of many troublesome species. These solutions are absorbed into the leaves and transferred through the phloem to the roots or other underground parts. Respiration is greatly accelerated. This speeding up of respiration depletes reserve foods but at the same time induces uncontrolled or unregulated growth and brings about death. Care must be used in applying these weed killers, for many cultivated ornamentals and garden vegetables are extremely susceptible and may be seriously damaged or killed. Not infrequently a breeze carries spray or dust considerable distances, causing unintentional damage to valuable plants.

Other Secretions. Aside from the various enzymes, auxins, and vitamins, which have more or less obvious uses to the plant producing them, there is a long list of other substances that belong in the category of secretions because they are produced by gland-like structures. Some of these, such as the nectar secreted by many flowers, have a distinct value to the species of plants but probably not to the individual. That is to say, the species benefits because the nectar is sought by insects that consequently transfer pollen from flower to flower, but the individual plant actually wastes some of its own food in the form of the sugary solution which is the substance of the nectar.

Probably in the same category are the numerous odorous secretions of plants. The functions of such secretions as the aromatic oils of mint, onion, eucalyptus, and geranium, to mention only a few, are in doubt. Some of them may even be by-products of metabolism with, at best, only incidental uses to the species. As yet, there is no satisfactory answer.

Genes and Secretions. Some corn plants become fifteen feet tall, while their equally healthy neighbors are dwarf, even when growing under the same conditions. In Chapter 2 it was pointed out that such differences, which cannot be attributed to environmental effects, are brought about by variations in the genes. The most exacting studies of some of the dwarf and tall strains of corn have shown that, so far as height is concerned, the differences are due to one gene which is active in the dwarf plants and not in the tall ones. It brings about the destruction of auxins almost as rapidly as they are formed, in this way greatly reducing the ability of the plant to grow.

This is not an isolated case, for many characteristics have been proved to be controlled in like manner. One other example will be sufficient illustration. The flowers of the common garden four-o'clock are white, pink, or red, depending on the amount of anthocyanin present. The white flowers have none, the pink ones a small amount, and the red ones are richly supplied. These differences are known to result from the presence of two genes active for anthocyanin formation in the red-flowered plants, one in the pink-flowered ones and none in those with white flowers.

Many other instances are known in which the genes control the production of enzymes or other secretions or in other ways affect the cell chemistry in plants. It now appears that their action largely, or possibly entirely, depends on chemical controls.

For this reason investigators are more and more thinking of the genes as very active compounds, each of which is capable of initiating chains of chemical reactions which, together, bring about the observed hereditary characteristics of plants and animals.

Summary. Foods furnish the building materials for both protoplasm and cell walls and the energy for all the vital processes in plants. The total of the chemical activities in protoplasm is called metabolism. The constructive phase is anabolism. It includes photosynthesis, fat synthesis, protein synthesis, secretion, assimilation and the building of cell walls. The destructive phase is catabolism, which is almost entirely limited to the processes of respiration and digestion. In the former, sugars are broken down, usually into carbon dioxide and water, releasing their energy. This energy is commonly used immediately in assimilation or in the forming of compounds used in the making of cell walls or in producing secretions. Excess foods beyond those used in metabolism become reserves in various plant cells.

Secretions produced by protoplasm play many roles in metabolism. Without digestive enzymes and their various actions, many foods could neither be used to release energy nor as building materials for the plant body; neither could they be carried from the places where they are formed to those cells which must have them for their own life processes. Without respiratory enzymes, which must release energy from food, life would cease at once. Without auxins and hormones, growth, organization of flowers, roots, leaves, and probably other structures, could not be carried on. Other secretions of plants, whose functions are not so well understood, are vitamins, aromatic substances, and numerous other materials, some of which occur in only occasional species, while others are almost universal.

SUPPLEMENTARY READINGS

Bonner and Galston, "Principles of Plant Physiology."
Curtis and Clark, "An Introduction to Plant Physiology."
Chibnall, "Protein Metabolism in Plants."
Guilliermond, "The Cytoplasm of the Plant Cell."
Hoagland, "Inorganic Nutrition of Plants."
Nord and Werkman, "Advances in Enzymology."
Schopfer, "Plants and Vitamins."

Chapter 5

CYCLES OF ENERGY AND NUTRIENTS

Energy is the capacity to do work. That which is used in life processes comes in the form of light from the sun. Then, after a time this energy leaves the realm of living things in the form of heat and dissipates into space. That is to say, it is lost and does not again take part in life processes.

The various *materials* that are used in the protoplasm, such as carbon, nitrogen, oxygen, hydrogen, sulfur, phosphorus, and many others, contrast sharply with energy, for when they are lost from the living plant or animal they usually return in a form that can be absorbed by plants and can again become a part of protoplasm.

Because of their key importance we shall study the following main topics in this chapter:

The Flow of Energy
The Carbon Cycle
The Nitrogen Cycle
Cycles of Other Nutrients

The Living Balance. A small goldfish in a jar of clear water may continue to live for several hours without special care. Eventually, however, it will begin to swim frequently to the surface of the water and gulp air into its mouth. After a time death may be expected to ensue, but if a suitable device is introduced early enough, causing air to bubble up, thereby driving off carbon dioxide and, at the same time permitting oxygen to dissolve in the water, the fish ceases to show indications of distress and again swims about in a quiet manner. The same results may be obtained if fresh, thoroughly aerated water is used to replace that in which the animal has been living.

The gulping action on the part of the fish is an indication of a considerable depletion of dissolved oxygen in the water and perhaps of an excess of carbon dioxide. These conditions interfere with the respiratory activities of the animal. This is the reason why a fresh supply of oxygen dissolved in the water soon relieves the symptoms.

If suitable green water plants are introduced into the jar with the fish and the jar is kept near a lighted window it becomes unnecessary to change the water or to aerate it as before. In fact, such a balanced aquarium may be sealed airtight and kept in good condition for several weeks, if it receives strong light but does not become overheated, as sometimes occurs in direct sunshine. Commonly, under these conditions the fish never shows symptoms of a reduced oxygen supply.

Students are frequently puzzled by this simple experiment. Such questions as, "How does the fish respire?" and "Where does its oxygen come from?" are usually the first to be asked, and as the aquarium continues to develop, questions arise as to how it is possible for the plants to grow sufficiently to supply the food eaten by the fish. In actual practice, the plants frequently thrive so well that they increase considerably beyond the amount eaten by the animal.

Recalling the facts that both the animal and the plant respire and that the green plant carries on photosynthesis under appropriate conditions, it should be possible to interpret the exchanges of oxygen and carbon dioxide, and the food relations

within this small closed community. But the activities of the plant extend far beyond these simple exchanges.

A survey of the different activities which occur even in a single plant in the course of a day may be so varied, so complex, and sometimes apparently so contradictory that they may leave us with a sense of confusion. One process, photosynthesis, is building carbohydrates; others are breaking down these foods and using their parts with still other substances that come from the soil, making proteins; somewhere else the molecules of carbohydrates are becoming rearranged in such a way as to make fats; and in every cell of the plant more or less food is being broken down continuously, providing the energy which keeps all of the multitudinous metabolic activities progressing. The entire picture is one of construction, rearrangement, and destruction, with a dynamic interplay of energy exchanges at every step. It might seem that these activities are largely working at cross purposes, one set always undoing what the other has done. An analysis of the situation, however, shows that life could not continue without all of them acting in sequence, thereby forming something of a cycle, as given materials are broken down, only to be used again in life processes. As an example, as conditions stand at present, the green plants of the earth are using, in the process of photosynthesis, about the same amount of carbon dioxide as the combined actions of the burning of fuels and the respiration of all plants and animals is providing. If all release of carbon dioxide were to cease, photosynthesis would soon stop. Likewise, if photosynthesis should be halted, food supplies would quickly be exhausted and sooner or later carbon dioxide would almost cease to be set free because life could not continue, and an equilibrium would be established. But with these two alternative sets of processes always active, each undoing what the other accomplishes, an equilibrium is never reached and both can continue indefinitely.

The Flow of Energy. Every chemical reaction involves not only new groupings of atoms but energy exchanges as well. Sometimes energy is required from an outside source to bring about the reaction, as when a test tube must be heated to induce a chemical change in its contents. Under other conditions, it is given off. As an example, the burning of fuels is the uniting of these substances with oxygen, with the evolution of heat.

It should be recalled that energy may take many forms such as light, heat, electricity, or chemical energy; that it may be either potential or kinetic; and that any form can be changed into any other by appropriate means.

The energy used in metabolism comes to the protoplasm by way of the process of photosynthesis, reaching the plant in kinetic form as light. In the carbohydrates it becomes inactive or potential and when other foods, such as fats or proteins are formed, it is passed on to their molecules. When assimilation occurs, building new protoplasm, some of the potential chemical energy of foods becomes kinetic and enters into the new set of reactions involved in the whirlpool of exchanges which occurs in life processes. Thus, the plant grows, gradually accumulating more and more energy by means of photosynthesis, but during the life of the plant some, usually in small amounts, takes the form of heat and is lost. When death comes, and if the plant should be burned, most of its potential energy becomes heat and the elaborate system built up in life is completely destroyed. If, on the other hand, it decays, much of its energy is transferred to the bacteria or other organisms which

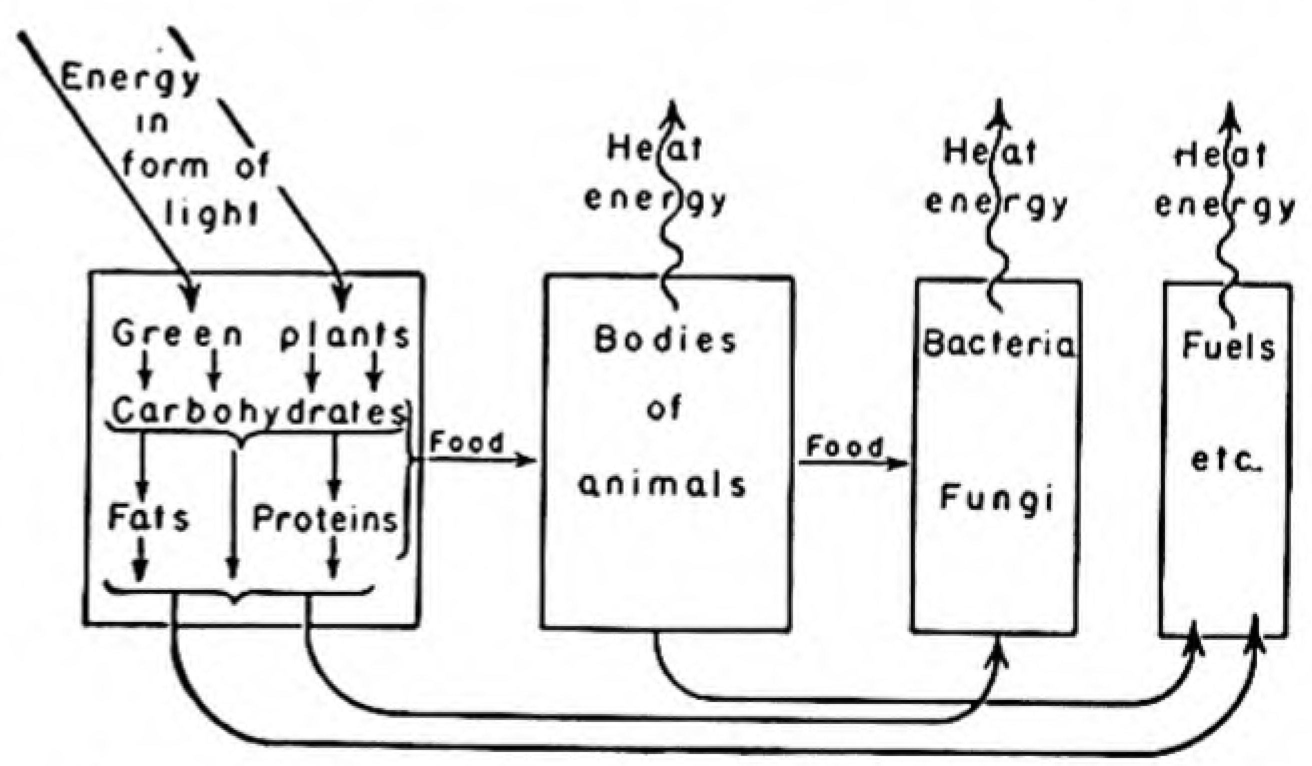


Diagram showing the main directions of energy transfer in living things.

bring about its decomposition, only to be lost eventually with their excretions or when they die. A similar series of steps is taken if the plant is eaten by an animal, because the nutrition of ani-

mals and of plants without chlorophyll is fundamentally the same.

To restate briefly, energy comes into living things from the sun by way of the process of photosynthesis, and after a longer or shorter period of time and a more or less complex series of transformations, it returns to the realm of the non-living. Sometimes this series of energy transformations is called a cycle, but there is no reason to suppose that the energy of the sun ever returns to it. Instead, it dissipates and is lost on the surface of the earth or into space, having played a role in life processes for a relatively brief space of time.

The Carbon Cycle. Carbon is present in all foods, and from food, in the process of assimilation, it becomes a part of the protoplasm. The carbon cycle may be thought of as beginning with photosynthesis when carbon dioxide and water are used as the non-energy-supplying raw materials from which carbohydrates are constructed. Such carbon compounds as carbohydrates, fats, and proteins are commonly called *organic substances*. It is in these that the energy used in metabolism is stored. Some carbon compounds contain large amounts, while others contain much less. In general, the higher the percentage of hydrogen atoms and the lower the percentage of oxygen in food, the greater the amount of energy which can be released in metabolism. As an example, compare starch and a fat. Both of these foods are constructed of carbon, hydrogen, and oxygen, but starch contains a much higher percentage of oxygen atoms than does a fat, and conversely, the fat has very much greater potential energy.

A given carbon atom may be shuttled about from carbohydrate to protein or fat and back again an untold number of times while it is within the protoplasm of a living plant. Eventually, however, it may leave the plant as a part of a molecule of carbon dioxide released in respiration. From this time on it is included in the carbon dioxide of the air, and, therefore, may be used again in photosynthesis. What other vicissitudes might befall a carbon atom residing in such a plant?

At this point the student should trace an atom of carbon through its cycle from a piece of burning coal or wood through the process of photosynthesis, into the protoplasm of an animal and back to carbon dioxide in the air. There is no single series of steps to be followed here. Instead, there are many possible activities into which carbon may enter. It is a rewarding exercise to follow a considerable number of these series.

The Supply of Carbon Dioxide. The amount of carbon dioxide in the air is very small—only three parts in 10,000—and green plants would grow better if the supply were greater. Photosynthesis decreases this amount, while respiration, together with all burning of plant and animal material, increases it. The greatest single source comes from the respiration of the myriads of bacteria that live in the soil, in fresh water, and in the sea. These microörganisms bring about the decay of organic materials everywhere, releasing most of the carbon of their organic compounds in the form of carbon dioxide. In this way the carbon that is trapped in organisms is set free and put into circulation where it may be used again.

Another set of processes having an influence upon the amount of carbon dioxide in the atmosphere results from the building up and tearing down of limestone. Limestone is calcium carbonate ($CaCO_3$), that is, the element calcium in combination with carbon and oxygen. When rainwater dissolves carbon dioxide from the air and then comes in contact with limestone, it changes the calcium carbonate to calcium bicarbonate ($Ca(HCO_3)_2$), which dissolves rather readily in the water and is often carried to the sea. In the sea, however, the reverse of this process may take place. There, myriads of animals, such as snails, clams, and oysters, together with smaller forms which have no well-known common names, get a part of the lime used in building their shells by changing the dissolved calcium bicarbonate to calcium carbonate. This action sets free half of the carbon dioxide, some of which diffuses out of the water and escapes into the air. Some aquatic animals go one step farther. The crayfishes, lobsters, crabs, etc., make their shells largely of calcium phosphate and thus may set free all of the carbon dioxide held by the calcium.

Today about three-fourths of the earth's surface is covered with water, but there have been

times in past geologic ages when the land surface was more extensive than it is now and other times when it was less so. Periods of extensive land exposure are characterized by widespread erosion of limestone and the robbing of the atmosphere of carbon dioxide. On the other hand, at times when the sea encroaches on the land, conditions are ideal for the growth of marine animals, and the air tends to become richer in carbon dioxide.

These two groups of processes concerned with the relations of carbon dioxide to limestone and to food, are so nearly balanced at present that, over the period of time in which there has been a science of chemistry, there has been no appreciable change in the carbon dioxide content of the atmosphere. But there have been times when conditions were different. A comparison of one of these periods with the present may help to make the point clear.

In the history of the earth, the Carboniferous period was one of the best for the growth of green plants. This was the period during which some of the great coal beds were laid down. The luxuriant growth of plants from which coal was formed came near the close of a long period when shallow inland seas covered most of what is now dry land. In these favorable places aquatic animals had been releasing carbon dioxide both by respiration and in the building of their shells which were later to be compacted into limestone. By this process and by volcanic activity, carbon dioxide is thought to have been released much more rapidly than it could be used by the limited growth of green land plants of the time, and it has been suggested that the air possibly contained 200 or 300 times as much carbon dioxide as it does today. Not only did this carbon dioxide provide the material for photosynthesis but it covered the earth like a blanket through which heat did not readily escape and tended to equalize temperatures, making even the polar regions warm. In this favorable environment the ferns and fernlike plants reached their climax in a long period of luxuriant growth. Photosynthesis stored enormous amounts of carbon in the bodies of the plants, which accumulated under mud and water in the swamps under conditions that prevented decay.

Geologic changes covered this mass of vegetable material with layers of sediment which compressed it into coal. It lies there now representing an impoverishment of the air and a quantity of stored energy.

The burning of coal releases, in the form of carbon dioxide, the stored carbon which entered those ancient plants as carbon dioxide and the potential energy which came to them as sunlight in a remote geologic age. From the standpoint of life problems, the coal age was one of nature's blunders, and the use of coal for fuel slowly turns back into the atmosphere some of the carbon dioxide which is so much needed for life. It should be recognized, however, that the amount is relatively very small for the best estimates indicate that all the coal mined throughout the world in a year's time would, when burned, produce considerably less than two-tenths of 1 per cent of the total carbon dioxide supply.

The Nitrogen Cycle. Another good example of the cyclic behavior of materials used by plants is that of nitrogen. Nitrogen as an element is comparatively plentiful. Four-fifths of the atmosphere is made up of it, and additional amounts are present in a great variety of compounds. But, in common with most of the elements, it is useful to the plant only when in chemical combination.

The nitrogen which is to enter into the composition of proteins in a green plant is usually absorbed from the soil in the form of dissolved *nitrates*. A

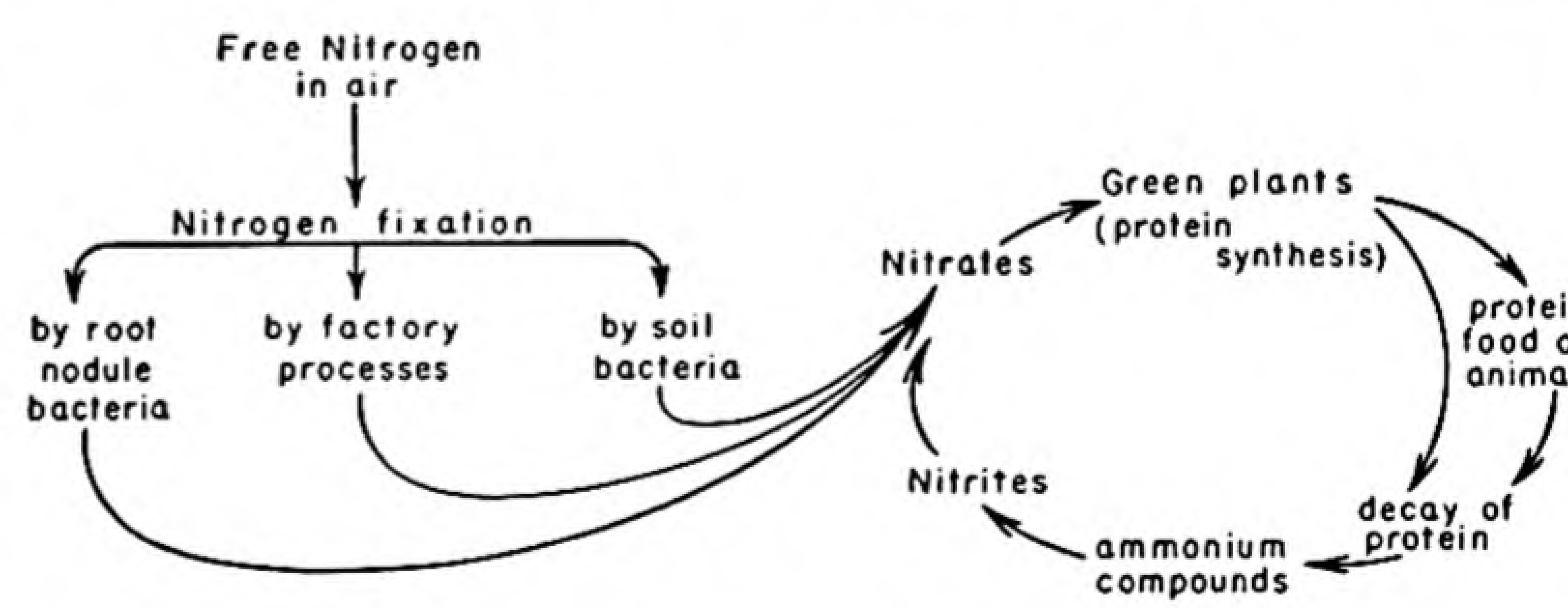


Diagram of the commoner steps in the nitrogen cycle.

nitrate is a compound of nitrogen with oxygen and such a base as potassium, sodium, or calcium. These various compounds are called potassium nitrate (KNO_3), sodium nitrate ($NaNO_3$), and

calcium nitrate ($Ca(NO_3)_2$), respectively. In all of these it will be noted that the potassium, sodium, or calcium is united to the combination, $—NO_3$. Such a group of atoms which acts as a unit is known as a chemical *radical* and $—NO_3$ is the *nitrate radical*. It is this radical rather than the entire compound that is important in the nitrogen cycle because it is absorbed and used independently in metabolism. It becomes incorporated into proteins, thereby leaving a nitrate deficit in the cell sap. But, following the laws of diffusion, more enters the roots from the soil. Potassium, sodium, and calcium, on the other hand, are used in much smaller amounts. Since these elements also follow the laws of diffusion the greater part of them remains in the soil.

PROTEIN SYNTHESIS. After the nitrate radical has been absorbed into the plant a series of steps ensues before the nitrogen is built into protein molecules. The details of the changes that take place are known only in part but experiments have shown that the *nitrate* ($—NO_3$) becomes *nitrite* ($—NO_2$); that the nitrogen then enters into the compound, *ammonium* (NH_3) which is changed quickly into the *amino radical* ($—NH_2$). This series of transformations occurs under the influence of one or more enzymes known as *reductases*.

The next step in the synthesis of proteins is the formation of amino acids. These substances always contain at least one amino group and a *carboxyl radical* ($—COOH$), which is derived from a sugar. Therefore, amino acid formation cannot occur except in places where both sugars and amino radicals are present.

There are at least 18 amino acids that are important in the nutrition of plants and animals, and in addition a few others are known. Each one is given a name. In the two formulae given below it should be noted that both the carboxyl and the amino radicals are combined with one or more other groups. The simplest amino acid is *glycine* with the formula: $CH_2(NH_2).COOH$. A more complex one is *lysine*, $CH_2(NH_2).CH_2.CH_2.CH_2.CH(NH_2).COOH$.

The various amino acids are frequently referred to as the "building stones" of proteins. The reason becomes evident from the following: After the amino acids have been organized from sugars and nitrates, a migration takes place to some growing part of the plant, such as a meristem or a developing fruit or seed. There, larger or smaller numbers of the amino acid molecules become linked together chemically, forming the giant molecules of proteins. As an example of the remarkable size of some of these, zein, from corn, has the formula, $C_{736}H_{1161}N_{184}O_{208}S_3$.

There are certain limitations in the way the amino acids can combine, but the number of possible combinations is staggering. Every cell is made up of an extremely large number of kinds of proteins and every species has certain kinds that are peculiar to it.

As long as a given protein remains a part of a living plant it may either take on an inactive form as a reserve food in a seed or fruit or it may be assimilated into the protoplasm where it will help to carry on the numerous life activities. So far as is known, animals must depend on plants for all their amino acids. In other words, the animal can rearrange them but cannot produce either the amino acids or the proteins from the raw materials. The plant, therefore, holds a key position in this cycle as well as in the carbon and energy series.

PROTEIN DEGRADATION. Up to this point the chief emphasis has been placed on processes of anabolism that build up the giant protein molecules from simpler compounds. But the protein molecule is subject also to many catabolic changes ranging from the loss of a few amino acid groups to a complete breakdown into simple inorganic substances. These down-grade changes are referred to collectively as the *degradation* of proteins.

In the healthy green plant the processes of degradation are not extensive. Instead, such products of destructive metabolism as are formed are resynthesized at once into new proteins with little or no loss of nitrogen to the plant.

UREA. If these proteins become the food of an animal a somewhat different series of events ensues. They are digested, being broken down into their constituent amino acids. These, in turn, are rearranged and assimilated into the protoplasm of the animal. The end products of protein catabolism in animals are carbon dioxide and urea, $(NH_2)_2CO$, or the closely related compound, uric acid,

$C_5H_4N_4O_3$. The average human being excretes about 20 Gm. of urea per day, and all animals, from the largest to the smallest, are continually losing nitrogen in this form. The aggregate amount from all sources is so great that urea is one of the most important compounds that returns nitrogen to the soil.

In the soil, urea is attacked by a group of bacteria which change it into ammonia (NH_3). The process is called *ammonification*. The acrid odor of a manure pile is due to the ammonia gas that is escaping into the air, released from urea and other nitrogenous compounds by the combined activities of a large number of kinds of bacteria and molds. If the ammonia is produced in the presence of water, much of it dissolves in the water or reacts with it to form ammonium hydroxide (NH_4OH) and remains in the soil, and most of that which escapes into the air is soon brought back to earth by rain.

Ammonia, in turn, is oxidized by *nitrifying bacteria* and the process is called *nitrification*. The energy released in this oxidation process is used in the metabolism of these organisms. The nitrogen of the ammonia molecule now becomes a part of the nitrite radical ($—NO_2$) which unites to form a compound with calcium, potassium, or sodium if these elements are present. Certain other soil bacteria oxidize the nitrites, forming nitrates ($—NO_3$) and releasing some additional energy which they use in their metabolism.

Ammonia and the nitrites are absorbed and used by plants to some extent, but unless they are very dilute they are harmful to the protoplasm. Their usefulness, therefore, is limited. Under usual conditions in the soil they are oxidized so quickly by the various nitrifying bacteria that they do not accumulate in more than very slight concentrations. The nitrates, on the other hand, can be used in large amounts by growing plants to build proteins.

DECAY. Protein disintegration follows one course other than that outlined above. When death comes to plants or animals, a great variety of bacteria in large numbers attack the various compounds that compose them. Among these invaders are many that bring about the decay of proteins. While there are considerable numbers of steps in this process, eventually such compounds as amino acids, ammonia, and carbon dioxide are formed. The amino acids and ammonia are oxidized in a series of steps, finally forming nitrates.

LOSSES OF FIXED NITROGEN. In swamps, peat bogs and other places where oxygen is largely excluded, certain anaerobic bacteria are able to reduce the nitrates ($—NO_3$) to nitrites ($—NO_2$) by removing one oxygen atom, and the nitrites to free nitrogen by taking away the remaining oxygen. This free nitrogen returns to the air where it is no longer available to living organisms. Such reduction is called *denitrification*. It occurs only slightly in well aerated soils.

A much more important loss occurs when ammonia gas escapes into the air and quickly diffuses far and wide. Although most of it is finally brought down by rain, much of it is likely to be carried in solution into the rivers and then into the sea where it is not available to plants that are important to man.

The nitrates and nitrites are, likewise, easily carried away in solution, to be used only in the metabolism of water plants or to be acted upon by the several kinds of bacteria mentioned above. For this reason, such commercial fertilizers as sodium nitrate and ammonium nitrate should never be applied to fields or lawns except at times when plants are growing vigorously. If applied at other times, the loss of combined nitrogen is very great before the plants become active and absorb it.

Another loss of combined nitrogen to living things came about in ancient times when certain mineral deposits were formed. At a number of places in the world, particularly in central Europe, in the desert regions of northern Chile, in parts of the arid Southwestern United States, and in various regions where there are limestone caves, there are extensive natural deposits of sodium or potassium nitrate (saltpetre), which are now being mined and used for fertilizer. The origin of some of this material is not known, but in other somewhat similar cases it is known to have been formed out of leachings from deposits of guano, the manure of birds or bats. As such, it is to be regarded as material which has been diverted from the nitrogen cycle and stored in places where it is not naturally

available to plants. Its present-day use as fertilizer is gradually bringing much of it back to the organic world.

In addition to the various losses described above, another kind of loss is chiefly the result of present day agricultural and marketing practice. A farmer in the Mississippi Valley raises a crop of corn, oats, wheat, or hay on a plot of ground. In one of two ways he can receive an income from his work and from his investment in the farm, the seed, and the necessary implements. He may take grain, hay, or other plant products to market or he may feed them to various farm animals, which in turn, must be sold. In either case large amounts of combined nitrogen are taken out of the soil and removed to distant places where they are consumed. With minor variations, the same kind of loss occurs on the western range lands where cattle and sheep are produced in large numbers to be shipped to distant markets, and where vegetables and fruit are grown in commercial quantities.

Nodules caused by nitrogen-fixing bacteria on roots of soybean. (Courtesy, U.S. Dept. Agr.)

GAINS IN FIXED NITROGEN. With all these losses of fixed nitrogen, the supply available to plants would soon be exhausted if it were not replenished in some way. At the present time both natural and artificial processes are involved in maintaining soil nitrogen. These fall chiefly into the two categories of *nitrification*, already discussed (p. 52), and *nitrogen fixation*, which brings new supplies into the cycle.

Any action that causes free nitrogen of the air to unite chemically with other elements, forming compounds, is called *nitrogen fixation*. Important forms will be discussed in succeeding paragraphs.

NITROGEN-FIXING BACTERIA. In the roots of most common leguminous plants there live certain kinds of bacteria which are able to combine atmospheric nitrogen with other substances, forming compounds which finally yield nitrates. Certain other bacteria that live free in the soil and are not associated with roots also have this power. Just how they do this, and what part nitrogen-fixation plays in the lives of these bacteria are as yet unanswered questions, but the results, so far as the fertility of the soil is concerned, are well known. The clovers, sweet clovers, alfalfa, soy beans, peanuts, and many other plants belonging to this family, have long been known to enrich the soil on which they grow, and the enrichment is roughly proportional to the amount of inoculation by these bacteria, as shown by the "nodules" on the roots.

There is a specific kind of bacterium for each of these crop plants, or for comparatively small groups of them, and, if bacteria of the right kind are not present in the soil, a leguminous plant not only has no advantage over any other, but grows very poorly. When there is any doubt as to whether the proper bacteria are present in the soil of a field in

which one of these plants is to be grown, the seed may be inoculated with a culture of them or the bacteria may be introduced by sprinkling over the field a small quantity of soil from a place in which the particular crop has been successfully grown.

Many "worn out farms" in some parts of the United States have been made highly productive by the introduction of a "rotation of crops" in which clover, vetch, or some other legume occupies a place. Such rotation takes various forms, but on a given field during a short series of years there are grown in definite order certain diverse crops, one of which is a legume. This crop furnishes hay and perhaps some pasturage before it is plowed under. Underground, it decays, setting free in the soil its rich stores of nitrogen compounds that result from the activities of the nitrogen-fixing bacteria in the roots. These compounds are likely to become gradually changed into nitrates. During a few succeeding years following the legume stage in such a rotation, the yields of other crops may be expected to be considerably increased in both quality and quantity. The only usual exception to this statement comes when one of the necessary elements other than nitrogen is deficient in the soil.

ELECTRICAL AND CHEMICAL FIXATION. Under natural conditions bacterial fixation is the chief means by which new nitrogen compounds are added to the soil and, therefore, to the nitrogen cycle. Modern technicians, however, are discovering numerous methods by which to produce nitrogenous compounds in such amounts and at such prices that they can be used profitably to replace a part of the nitrogen lost in agricultural practices.

The three most important of these factory methods are the *electric arc process*, the *cyanamide process* and the *Haber-Bosch* process. The first of these requires a great deal of electric current and is not economically feasible except where electricity can be generated at very low cost. At present it is used successfully in Norway because of abundant water power. By this method nitrogen and oxygen from the air are directly united into nitric oxide (NO) in the extremely high temperature of a large electric arc. Subsequent treatments change this compound into sodium nitrate ($NaNO_3$), a valuable fertilizer.

The cyanamide process also requires relatively cheap electric energy by which calcium carbide (CaC_2) is caused to unite directly with nitrogen gas, forming calcium cyanamide ($CaCN_2$) and carbon as follows:

$$\underset{\text{Calcium carbide}}{CaC_2} + \underset{\text{Nitrogen}}{N_2} \rightarrow \underset{\text{Calcium cyanamide}}{CaCN_2} + \underset{\text{Carbon}}{C}$$

It is manufactured chiefly in the United States, Canada, and Germany. In the soil this product undergoes a series of changes, eventually forming ammonia, then nitrites and finally nitrates.

The Haber-Bosch process is different from the two electrical ones just described in that catalysts (chemical activators), rather than extreme heat, bring about the direct synthesis of ammonia (NH_3) from nitrogen and hydrogen gases. Once started, the heat of the reaction is sufficient to keep it in progress and further outside energy is not required. Large quantities of ammonia and its derivatives are manufactured by this method in England, Germany, and Japan.

Whatever the steps taken in nitrogen fixation, whether they are brought about by bacterial action, or by the manufacturer's use of electrical or chemical synthesis in the production of fertilizers, atmospheric nitrogen becomes incorporated into living protoplasm. From the time the free nitrogen of the air has been united with oxygen or hydrogen, it is drawn into the nitrogen cycle. There it remains until, perchance, it may be released again as free nitrogen by the action of denitrifying bacteria.

BALANCING THE NITROGEN BUDGET. Down through the ages decaying organic materials have continually returned their substance to the soil, maintaining its fertility, while nitrogen-fixing organisms have slowly added to the total fixed nitrogen supply. With the advent of agriculture, however, losses of fixed nitrogen began to occur both because of the removal of crops and because tillage caused the rich top soil to wash away. These losses tended to overtake gains, and cultivated soil became less productive. The farmer, even in ancient times, learned to enrich the soil by the application of waste materials from plants and animals. The histories of the most primitive agricultural peoples

show that they knew the value of various kinds of manures, decayed leaves, or the bodies of such animals as fish for fertilizers. They did not, of course, know why these substances were useful, but they knew that they produced beneficial results. Wastes of this kind contain other nutrients than combined or fixed nitrogen, but the most spectacular results produced by them are doubtless due to that element.

The well-trained, alert, present-day farmer is aware of the causes of reduced soil fertility and he uses every means available to replace losses. While others are careless, he saves and uses all the barnyard manures, decaying straw, corn stalks, and other residues; he rotates his crops, including in the series some member of the clover family and, when needed, adds commercial fertilizers that correct deficiencies and replace the losses from his soil due to the removal of crops.

Cycles of Other Nutrients. Other elements such as phosphorus, sulfur, potassium, or calcium, necessary for the welfare of ordinary plants, can be shown to move in cycles comparable with that of nitrogen. The cycles of the other nutrients are, however, usually simpler than that of nitrogen and, since they are required in very much smaller quantities or are more often present in sufficient amounts, they attract less attention.

Summary. The atoms of carbon, oxygen, hydrogen, sulfur, phosphorus, and in fact all of the nutrient elements used by plants and animals in their metabolism, alternate between the organic and inorganic states, being first a part of some living thing and then of the air or of a soil mineral, and back again. Energy, on the other hand, comes to living things by way of sunlight and is lost to them as heat, in which form it dissipates into outer space.

SUPPLEMENTARY READINGS

Bonner and Galston, "Principles of Plant Physiology."
Chibnall, "Protein Metabolism in Plants."
Curtis and Clark, "An Introduction to Plant Physiology."
Hoagland, "Inorganic Nutrition of Plants."
"Hunger Signs in Crops," a symposium.
Meyer and Anderson, "Plant Physiology."
Miller, "Plant Physiology."

Chapter 6

THE WATER RELATIONS OF PLANTS

Any land plant made up of roots, stem, and leaves acts as a channel through which water travels from soil to air. Transpiration is the chief process by which water is lost from such a plant. The water that is used and lost tends to be replaced by absorption through the roots.

Water and Plants. The early settlers in the semiarid West met some situations that were indescribably discouraging. These farmers brought with them the crops with which they had been familiar in the more humid climates farther east. They were soon to learn by hard experience that they must find more suitable plants to cultivate in these new conditions, but before they had had time to make this discovery a series of tragedies befell them. They planted corn in the spring as was their custom. Early rains and the rich virgin soil conspired to give promise of fine yields. Then, in midsummer, there came the hot, dry winds experienced occasionally in semiarid and arid regions. In a few hours these fields of shoulder-high corn were dead, dry, shreds of shriveled leaves and spongy, immature stalks sprawling over the ground.

The desperate plight of the farmers and their families must be left to the imagination, but the interpretation of the causes of the destruction of the corn plants lies within the province of this chapter.

In order to have a clear picture of the stresses to which these fields of corn were subjected by the hot winds, one needs only to visualize a plant with its roots surrounded by moist soil and with every condition suitable for rapid growth, when a powerful dry wind at high temperature began to sweep

over it. Evaporation from leaf and stem was vastly increased and finally the plant died from drying, because absorption of water through the roots fell far short of the amount necessary to replace that which was carried away by the wind.

This is an extreme example but it well illustrates a general situation. Ordinary plants absorb water through the roots and lose much of it by evaporation from the leaves into the air. When intake does not keep pace with loss, a more or less powerful stress results which may or may not be great enough to bring death. The following discussion will make clear the principles involved.

Study of transpiration. Roots and soil sealed in watertight container; transpiration loss determined by weight. (*Below, left*) Small vessel with free water surface for comparison.

TRANSPIRATION

Water Losses. Moisture will always evaporate from any wet surface in contact with air that is not fully saturated with water vapor. All living cells surrounding intercellular spaces in the mesophyll or in any other part of a plant in air are constantly covered with a film of moisture. From the very nature of plant structure, therefore, water continually evaporates more or less rapidly from all the aerial parts. Only a very small fraction of the water required for the welfare of a plant is actually used in metabolism. The greater portion of it simply enters the roots, passes up through the stem, and escapes into the air in the form of vapor. The loss of water vapor from the plant is known as *transpiration*.

It should be clear from the foregoing discussion that transpiration is inevitable in active green leaves in the air, because the mesophyll cells are always moist and the intercellular spaces in contact with these moist walls contain air. Evaporation occurs, therefore, and the vapor diffuses out, chiefly through the stomata. How could photosynthesis take place in leaves in the air without the loss of water vapor?

Amounts Lost. Various methods are used in measuring or estimating the amounts of water that escape from a growing plant. One of the most reliable is to seal the roots in the soil in a watertight container, with the leafy shoot extending into the air. With this arrangement no vapor can escape except through the exposed stem and leaves. By weighing it is possible to determine with a high degree of accuracy the amount of water loss in any given period of time. Thus a single corn plant has been found to lose 54 gals. of water during its growing season. On this basis, the vapor transpired from an acre of growing corn is estimated to amount to 1700 tons per season. This amount, if standing as liquid water on the land at one time, would be about 11 inches deep.

A less reliable method must be used with large

trees or other plants that cannot be weighed while they are growing. The most common means of estimating transpiration under these conditions is to place leafy cuttings in water and to determine the loss in weight. From this information some idea can be gained of the transpiration from the entire plant. With sufficient masses of such data it is possible to make reasonably accurate estimates, but the fact that the leafy shoots are detached from the roots probably introduces a considerable factor of error. A few estimates made in this way are given as examples. A birch tree standing alone in the open loses 75 to 100 gals. per day in midsummer, while mature apple trees transpire 600 tons per acre per day and a field of grass or clover gives off 500 to 750 tons per acre per season.

Where soil moisture is somewhat limited and the air is hot and dry, as in the example given at the beginning of this chapter, a serious water deficit may occur in the tissues. In fact, one of the greatest causes of plant death the world over comes from the inability of many individuals to balance water loss with sufficient intake.

In the light of all that has been said above, it should be evident that the rooted plant acts as a pump, continually removing water from the soil. So effective is this pumping action that the water table (the standing water in the soil) fluctuates considerably during a growing season or even during the day. As an example, the water level in a well in an alfalfa field was found to fall 2.5 inches during the day and regain as much at night when transpiration is greatly reduced. It should be understood that the combination of lower temperature with the resulting considerable increase in relative humidity and the closure of stomata conspire to reduce transpiration rates at night.

Clearly the weed is not only unsightly in cultivated ground, but it is a competitor of crop plants. It competes for water and also for soil nutrients, and when the crop is young, for light as well. All these factors reduce the growth and hence the value of the cultivated plants.

So keen is the competition for water that a weedless fallow field is often moist and friable while similar soil under a dense plant cover is dry and cloddy. Advantage is taken of this fact in certain regions where the annual rainfall is not sufficient to grow good crops. Here the *summer fallow* is used successfully. After harvest, various means are employed to break the surface soil and all plant remains into a fine, mulchlike layer. During the ensuing year all precipitation soaks into the ground, where it is held by the soil colloids. Frequent shallow cultivation by various means prevents the growth of weeds. In this way a supply of water is added by rain and snow but almost none is lost through transpiration. Thus it is possible to raise excellent crops every second or third growing season.

So important is water in the growth of plants and therefore in the livelihood of people that the various states in the more arid parts of the United States must reach agreements with their neighbors on water rights. Without irrigation water, large food-producing areas could be only sparsely inhabited. Such is the demand for water in these regions that hydrologists must keep close watch on the height of the water table and restrict use whenever the supply begins to fall too low for safety. Water on farm lands, then, is a commodity that is highly prized by those who know its worth.

Within recent years there has been a gradual increase in the use of irrigation, especially during periods of drought, even in humid climates. Various means are continually being devised to catch and hold in the soil as much of the rainfall as possible. The Soil Conservation Service of the Department of Agriculture is especially active in both research and application of methods of water storage in the soil. Obviously, water that soaks into the ground does not wash the nutrients away. Thus a double purpose is attained, because both soil and water are kept where they can be most useful.

Plants Classed as to Water Requirements. In an earlier chapter (p. 31) it was stated that plants may be classified on the basis of their water requirements as hydrophytes, mesophytes, and xerophytes. A hydrophyte that lives under water obviously is not subjected to transpiration; if its leaves are in the air there is a certain amount of water loss, but because the air over a body of water always remains moist, evaporation from plant tissues takes place very slowly.

The mesophyte thrives best in soil that is only moist and with its leaves in air that is usually moderately humid. Under these conditions transpiration takes place at a relatively slow rate, with absorption supplying water as fast as it is lost by evaporation. Whenever high temperature and extremely low humidity occur, especially if these are accompanied by wind, the tissues are likely to lose water in such large amounts that absorption through the roots does not take place rapidly enough to replace that which is lost. If this lack of balance between intake and outgo is of brief duration, no apparent ill effects result, but if it continues, first wilting and then death and complete drying may ensue, as in the corn plants described above.

When xerophytes are subjected to these same conditions, they merely cease to grow until a change in weather permits the reëstablishment of a better balance. Normal activities are then resumed with no apparent harm to the organism.

Factors that Retard Transpiration. The leaves of a maple tree growing near a pond lose water by evaporation much less rapidly than an equal area of the surface of the open water. It is obvious, therefore, that the structure of the leaf is such that evaporation from its surface is restricted. This is true for all types of leaves growing in air. Comparison of measured leaf areas with equal surfaces of water in open vessels shows that evaporation may be as much as 20 times as great from the vessel as from the leaf. The rate varies greatly with the kind of plant used and the conditions of the experiment.

A number of factors may operate to exercise this control of transpiration and while none of them is mechanically perfect, together they work with practical efficiency under ordinary conditions.

THE EPIDERMIS. If the epidermis is removed from a part of the leaf, the underlying tissues soon dry and die. Evaporation has been found to take place from 15 to 24 or more times as rapidly from leaves with the epidermis removed as from those which have it intact.

The efficiency of the epidermis in this respect can be accounted for, in part, by its structure. Its cells are comparatively thick-walled and are fitted together, with no spaces between them except the stomata. The outer wall of each epidermal cell is usually much thicker than the others, and it is commonly reinforced on the outside by an extra layer, the *cuticle*, which is made of fatty materials having special waterproofing qualities. This effect seems occasionally to be further increased by an additional coating of fine granules of *wax*.

STOMATA AND TRANSPIRATION. The stomata constitute the greatest obstacle to the complete control of transpiration by the epidermis. Any hole through the epidermis will permit some evaporation, and stomata are essentially holes. But a part of the disadvantage is overcome by the fact that the guard cells are so constructed that, under varying conditions, they open and close the pore between them. There are different kinds of guard cells, and they work in several different ways. But in general any condition which brings about the absorption of water into them causes the stoma to open. It would seem, then, that the stomata would open when the air was moist and close when it was dry, and the mesophyll cells would be protected when they needed protection. But there are other influences which may affect the absorption of water into the guard cells, and some of them operate in a manner directly opposite to what would be expected. It has been observed, for example, that the stomata of many plants tend to open in the light and close in the dark, although the air is usually more humid at night than it is during the day. Why should they behave in this apparently contradictory manner? A simple answer to this question is impossible, as will be evident from the discussion on succeeding pages.

Mention has been made of the fact that the guard cells contain plastids. These are somewhat green in color and are often considered to be true chloroplasts but within the past few years some experiments have thrown doubt on their exact character. Nevertheless, when they are in the light they bring about a marked increase in the concentration of sugar in the guard cells by some means as yet not fully understood. Dissolved substances in any cell tend to cause water to enter from neighboring sources. In this case water diffuses in from those that are adjacent, causing the guard

cells to stretch. This action opens the stoma. When darkness comes on, the sugar in the cell sap is, for the most part, changed into starch. Since starch does not dissolve in water, the excess water in the guard cells diffuses out into the cells from which it came. In this way the tension within the guard cells is reduced and the stoma closes.

WILTING AND TRANSPIRATION. Under conditions of drought, another factor enters the situation in such a way as to protect the plant from drying. When leaves wilt, the guard cells often wilt along with their neighbors, closing the stomata, thereby greatly lessening the rate of transpiration. From these facts it becomes evident, that the amount of stomatal opening when the plant is in the light is the resultant of two opposing forces: First, light tends to cause the stomata to open, and second, this action increases transpiration, which may become rapid enough to induce wilting with its tendency to close them.

Corn plant showing the characteristic rolling of edges of wilting leaves. Photograph taken during period of drought.

Possibly this discussion oversimplifies the explanation. Very accurate studies of the behavior of stomata show that different species of plants behave very differently under the same conditions. Thus, stomata of some plants, such as the potato, close only a short time during the 24 hours of a day, while the guard cells of some other plants are lignified (woody) and cannot move at all.

When attempting to interpret the opening and closing of stomata, students too often take the easy but inaccurate way of saying: "The stomata open when they need to open to let in carbon dioxide, and close when photosynthesis can no longer take place." To what extent is this statement true? Under what conditions is it untrue? Would it be possible for the closing of stomata to retard photosynthesis?

SPECIAL LEAF CHARACTERISTICS. In many plants the leaves roll or fold in such a way that they present a reduced surface to the air, especially when it is dry. As an example, the outer edges of corn leaves first turn upward and then continue to turn inward forming closer and closer rolls as they become progressively more wilted in times of drought or hot, dry winds. By such mechanical action the upper epidermis and, with it, many or all the stomata are somewhat protected and presumably transpiration is reduced. This mechanism is especially well developed in almost all members of the grass family. Here, there are usually longitudinal strips of *bulliform cells* that lose moisture and shrink when exposed to dry air. When, as in bluegrass, these specialized motor cells occur in long lines near the midrib, the leaf folds together like the pages of a book, as shown in the illustration on p. 31, but where there are numerous strips parallel with the veins, as in corn, the leaves roll.

Many desert plants have leaves that are very small; some hold them for only a few days and then drop them; others have no functional leaves, their foliage being represented by horny scales; still others have thick, leathery leaves heavily coated with cuticle. Some desert plants, especially certain species of cactus, have no foliage at all, the green parts being modified stems. All these plants have relatively small transpiring surfaces and the rate of evaporation is thus correspondingly slow.

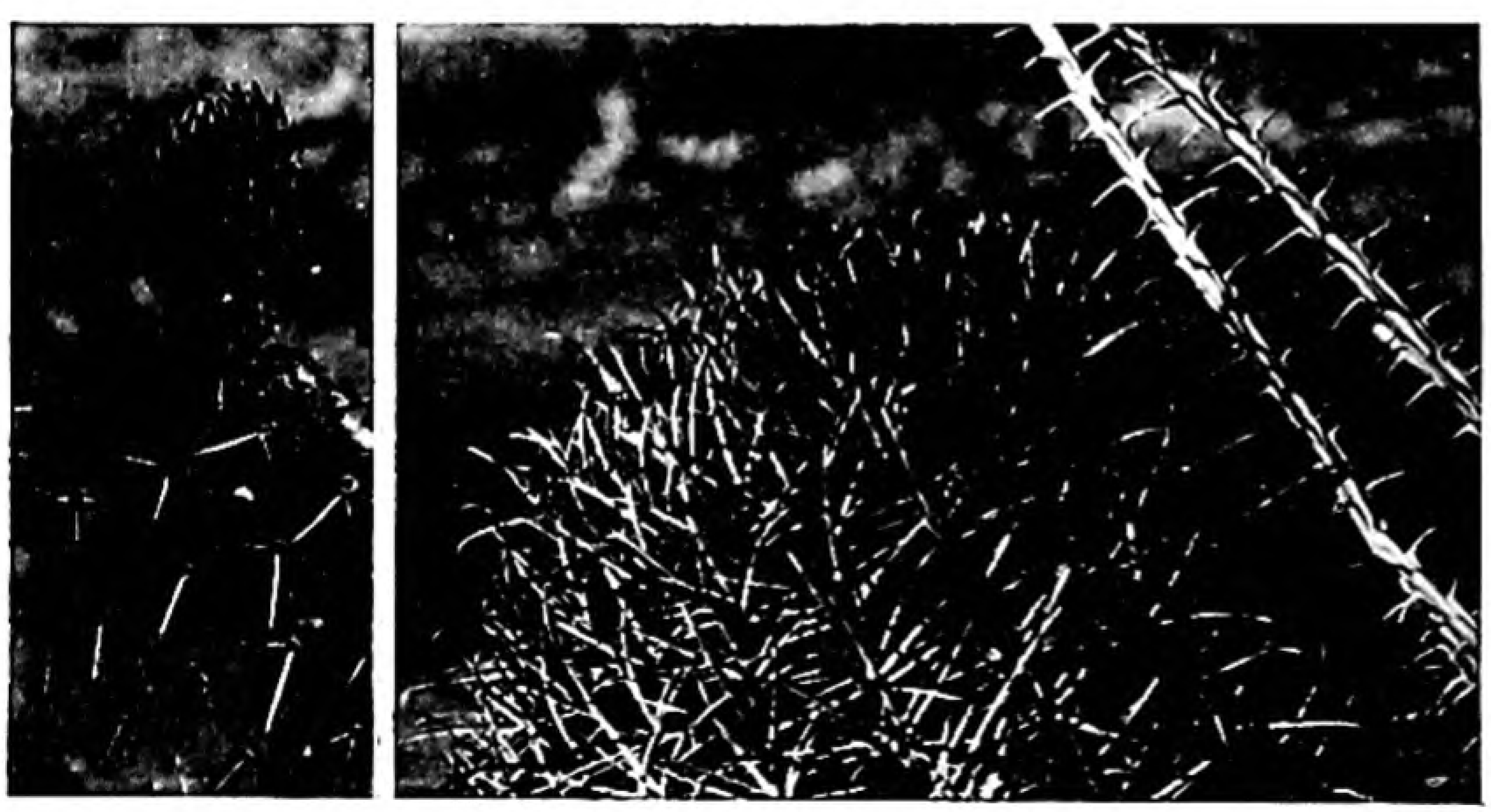
Cell Colloids. Another type of control of transpiration results from the very nature of the colloidal materials which make up the contents of the cells of many xerophytes. In these, proteins and carbohydrates imbibe large amounts of water and take on a jellylike consistency. A powerful resistance to the loss of imbibed water develops. Evaporation takes place very slowly, therefore, especially when the supply of moisture in the plant becomes somewhat reduced.

In desert succulents such as cacti and century plants the cells contain a large amount of colloidal material and the plants are covered with a very thick epidermis. These two factors acting together all but prevent transpiration. Although the colloids give up water slowly, they have the ability to imbibe it rapidly when the soil is moist. The giant cactus of southern Arizona has a fluted stem which opens out, accordionlike, when rains follow a long period of drought, and the roots absorb water from the wet soil. Because of the various controls of transpiration one of these plants lost only a quarter of its weight during a year after it had been uprooted and taken to a dry laboratory room and given no care.

These and other desert plants often flower freely and produce fruits with their roots embedded in soil so dry that absorption is impossible. The necessary water for such activities comes from their reserves in their colloidal cell contents.

Resistance to Water Movement. One of the most powerful influences retarding transpiration is not, properly speaking, a control at all, but is a result of purely physical conditions in the soil and plant. Briefly, it is this: When soil moisture decreases to the point where absorption through the roots is considerably reduced, there gradually develops a resistance to water movement into the plant, and a consequent check on transpiration ensues. The plant acts as a channel through which the water is drawn out of the soil, and when it enters the roots only slowly, it travels through the plant at a restricted rate, reaches the transpiring surfaces in small amounts and, therefore, cannot evaporate rapidly. This is an important reason why transpiration from all kinds of plants is greatly reduced, as it almost always is, when the soil becomes gradually drier during a drought.

Why There Is No Complete Control. It should be noticed that all except the last two of these restrictions on transpiration have consisted in preventing the free access of the air to the photosynthetic tissue of the leaf. Since carbon di-



Desert plants with reduced leaf surface or without leaves. (*Top*) *Ephedra*, a switch plant with functionless scale leaves. (*Bottom, left*) Prickley pear cactus with temporary leaves on young flat branch at top. These leaves fall off after a few days. Note old leafless part below, with thorns at leaf scars. (*Bottom, right*) Top of barrel cactus, which never produces leaves, and two slender, thorny stems of ocotillo. This shrub occasionally has numerous broad, flat leaves which soon fall off.

oxide from the air cannot reach the chloroplasts within the cells except by going into solution, photosynthesis could not take place effectively if the walls of the chlorophyll-bearing cells did not display a wet surface to the atmosphere within the intercellular spaces. But when moisture comes into contact with dry air, evaporation is certain to occur, and the vapor diffuses out through the stomata. Transpiration, then, seems to be a sort of necessary evil; an evil so great that it causes the death of thousands of plants during every period of extended drought. Apparently it does the plant little or no direct good, and yet the plant cannot produce the food which it must have to live without losing water by transpiration. The structure of the leaves of land plants permits the rather free entrance of carbon dioxide while it considerably retards transpiration. Because this situation is a compromise between two antagonistic forces, the plant with its shoot in air cannot reach a maximum efficiency in either photosynthesis or in protecting itself from loss of water.

Mullein plant showing thick, feltlike coat of hairs.

The ideal situation, if one may judge from growth rates of plants, is that in which the leaves are surrounded with air which is so moist that it has little drying effect. Under conditions like this, little control of transpiration is necessary, the green tissue has free contact with the air, and photosynthesis goes on at full speed all day long.

Trichomes. The covering of hairs (*trichomes*) which occurs on many leaves has been supposed to retard transpiration. It has been assumed that scattered hairs probably have little influence, but that the more abundant growths, reaching the limit in such plants as mullein, must give a certain amount of protection by preventing the movement of a layer of air in contact with the epidermis. In some plants the hairs are modified into the form of flat, overlapping scales which are thought to give protection without excluding the air. Some plants have the stomata set at the bottoms of deep pits in the leaf, and the pits are often partly clogged with a growth of hairs. All such structural peculiarities as these so strongly suggest protective functions that it is easy to interpret them as having such definite values without any actual proof. The only sure way of finding out how useful they are is by means of carefully conducted experiments, and in most instances these are yet to be made. A few such studies which have been carried out, however, have given little or no proof that these structures bring about any considerable reduction of transpiration.

A few years ago an investigator shaved the thick, matted, feltlike coat of hairs from the leaves of potted mullein plants, comparing the transpiration losses before and after the hairs were removed. His statistics showed a slight decrease in transpiration with the loss of the coat. The conclusion would be, therefore, that if the woolly covering over mullein leaves has any function at all it must relate to some activity other than transpiration.

Future investigations may prove that trichomes have value in the life of plants that possess them, but at present such structures seem to be unimportant products of chance gene combinations.

In other words it would seem that these plants inherit the ability to produce such hairy outgrowths, but that these coats neither help nor hinder the life processes. This interpretation is supported by the fact that hairy and hairless plants often appear to survive equally well when growing together even under hard living conditions.

Positive Values Attributed to Transpiration. For many years a few botanists have thought that transpiration had some definite, positive value to the plant, and was not merely an unavoidable incident. One argument has been that anything that occurs so extensively must have value. Is that sound reasoning? Here, as in all other scientific theory, the final answer to the questions involved must come from accurate observation and especially from carefully planned and expertly executed experimentation.

TEMPERATURE CONTROL. It has been assumed that transpiration is of advantage because evaporation of water lowers the temperature of the leaf and prevents overheating; that is, that transpiration is a sort of plant perspiration. As reasonable as this theory is, experimental evidence does not support it. It is a well-known physical fact that the evaporation of water does cool the leaf because evaporation always lowers temperature. But it is questionable whether this cooling effect is of any very great significance. One worker finds, for instance, that transpiring leaves are only 2° C. to 4° C. cooler than leaves which are not transpiring but are otherwise kept under the same conditions. In agreement with this finding, the majority of species which grow in the desert where danger of overheating is extremely great, transpire far less than other plants, especially when there is little soil moisture. Cactus, for instance, transpires very little, and that at night when temperatures are relatively low.

This apparent anomaly is explained readily by the following outline of the events that are likely to ensue when light strikes a leaf:

1. An average of about 25 per cent is reflected from the surface, having no effects on the leaf.
2. A small percentage passes through the tissues as light, producing no effects.
3. About 3 per cent is changed into potential energy in the process of photosynthesis.
4. Much of the remaining light energy takes the form of heat. Of this, (a), the major part radiates so rapidly from the leaf surface into the surrounding air that the tissues are only slightly affected, and (b), a small fraction causes water to evaporate, that is, brings about transpiration.

ASCENT OF SAP. Another advantage sometimes attributed to transpiration is that it is one of the factors responsible for the ascent of water through the stem of the plant. Some have believed that this movement of water is necessary to bring minerals from the roots to the leaves and growing parts where they are to be used. Thinking along this line has probably been influenced a great deal by the idea that plants need to have a kind of "circulation" like that of the blood of animals. But the movement of the very small amounts of minerals that must pass from the roots up into the shoot of a plant is very different from that of the vast loads of food, water, oxygen, and wastes throughout the body of an animal. The comparison is far more misleading than illuminating. Recent work indicates that minerals from the soil may not be transferred primarily through the water tubes, and that the transpiration stream is not responsible for the rapid movement of these substances. The minerals seem rather to travel chiefly through the phloem, entirely independent of the upward motion of water in the water tubes of the xylem.

Finally, at least one situation in nature points rather definitely to the uselessness of transpiration as a plant function. In certain parts of the world, as in the tropical forest belts where rainy seasons prevail, there are long periods when the air is so nearly saturated with water vapor that there is little or no transpiration from the leaves of the plants. Yet those regions support the most luxuriant vegetation in the world. How do the plants which grow there keep cool and carry minerals upward? Although the conditions of growth are somewhat different, the same questions may be asked about plants which grow completely submerged in water. These plants do not transpire, and it has been shown experimentally that there is little or no movement of liquids along their stems. Yet absence of transpiration does not seem to harm these water plants. Transpiration from leaves of land

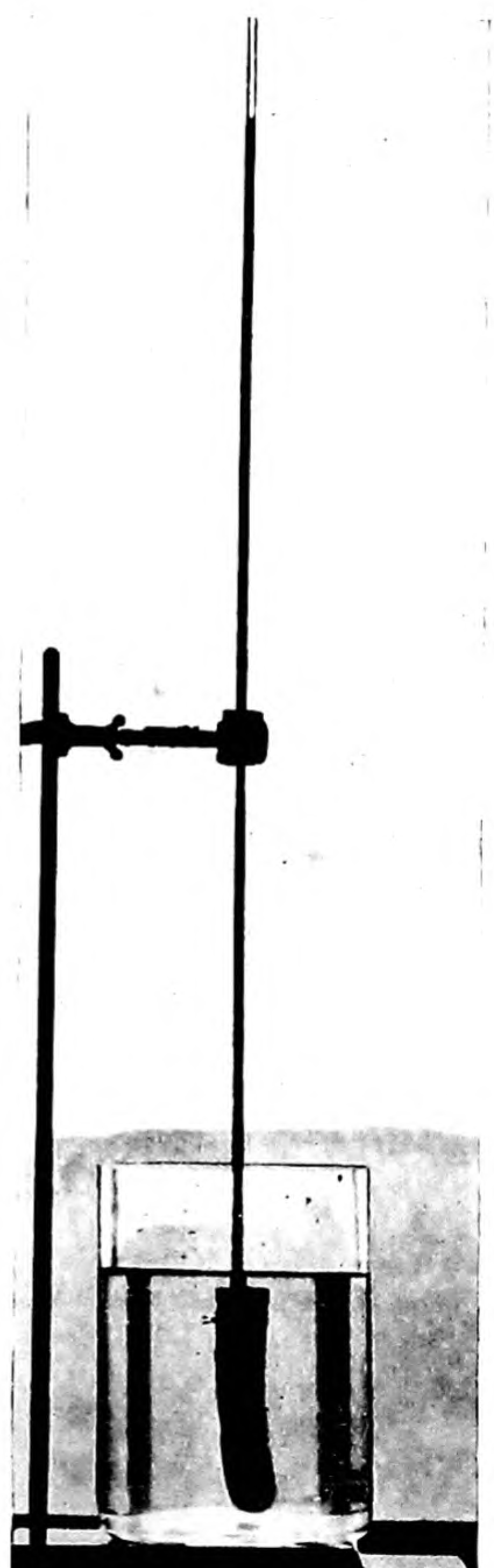
plants, then, seems to be simply the evaporation of water from the moist surfaces which are exposed to air within the intercellular spaces.

ABSORPTION

Any growing plant must absorb enough water to replace the amount lost by transpiration plus that used in all phases of metabolism. All this water and the various minerals in solution have no other place of entrance into common land plants than through the younger portions of the roots, because other parts usually have waterproof coverings of cork or cutin.

As the leaf is the primary photosynthetic organ, so the root tip is a highly specialized organ of absorption and transfer.

The Driving Forces in Absorption. To a large extent absorption is the process of *osmosis*, and osmosis may be defined as *differential diffusion through a semipermeable membrane*. In order to interpret this statement the student should recall the laws of diffusion discussed in Chapter 3, for this is the same type of phenomenon occurring under somewhat different conditions. Water and dissolved substances follow the same laws of diffusion as those governing gases, that is, *any diffusing substance travels from the greater to the lesser concentration of itself*. But in osmosis, diffusion is complicated by the presence of a semipermeable membrane. A semipermeable membrane is one through which certain substances can pass readily while others can pass little or not at all. Osmosis occurs when such a membrane separates two diffusible substances one of which can readily penetrate the membrane while the other cannot. This type of behavior may be illustrated by a common laboratory experiment. A solution of sugar (syrup) is placed in a diffusion shell which is an artificial membrane that is freely permeable to water but through which sugar can pass only slightly. A glass tube is provided as an outlet and the diffusion shell is supported in a vessel of water. The sugar solution slowly rises in the tube. There can be but one explanation of this action—water travels through the membrane and thus increases the volume of liquid inside. Applying the laws of diffusion, the explanation becomes possible. Outside the membrane the water is approximately 100 per cent pure while inside, a high percentage of sugar replaces a corresponding amount of water. As a consequence, the percentage of water inside is less than 100. Following the laws of diffusion, water moves through the membrane



Osmoscope, illustrating rise of water in outlet tube. The battery jar contains water, and the semipermeable diffusion shell suspended in it contains a dark syrup.

from its higher (100 per cent) to its lower concentration. Since sugar can not diffuse outward because the membrane is impermeable to it, the net result is that water enters but sugar cannot leave and the volume inside the diffusion shell increases, causing the liquid to rise in the outlet tube.

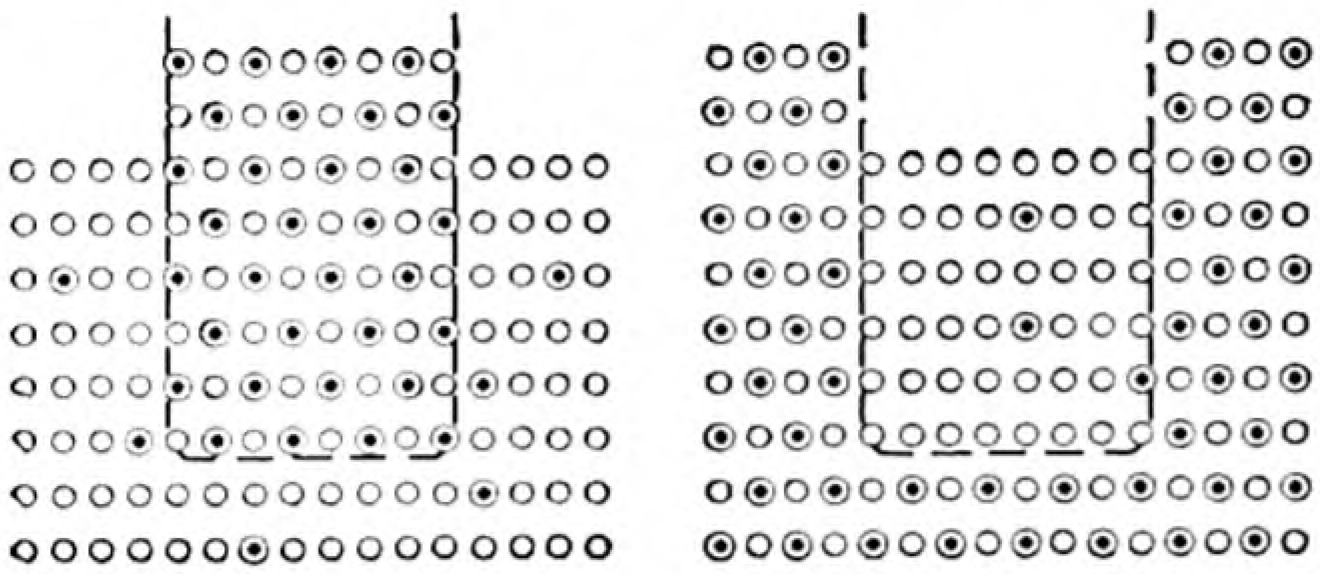
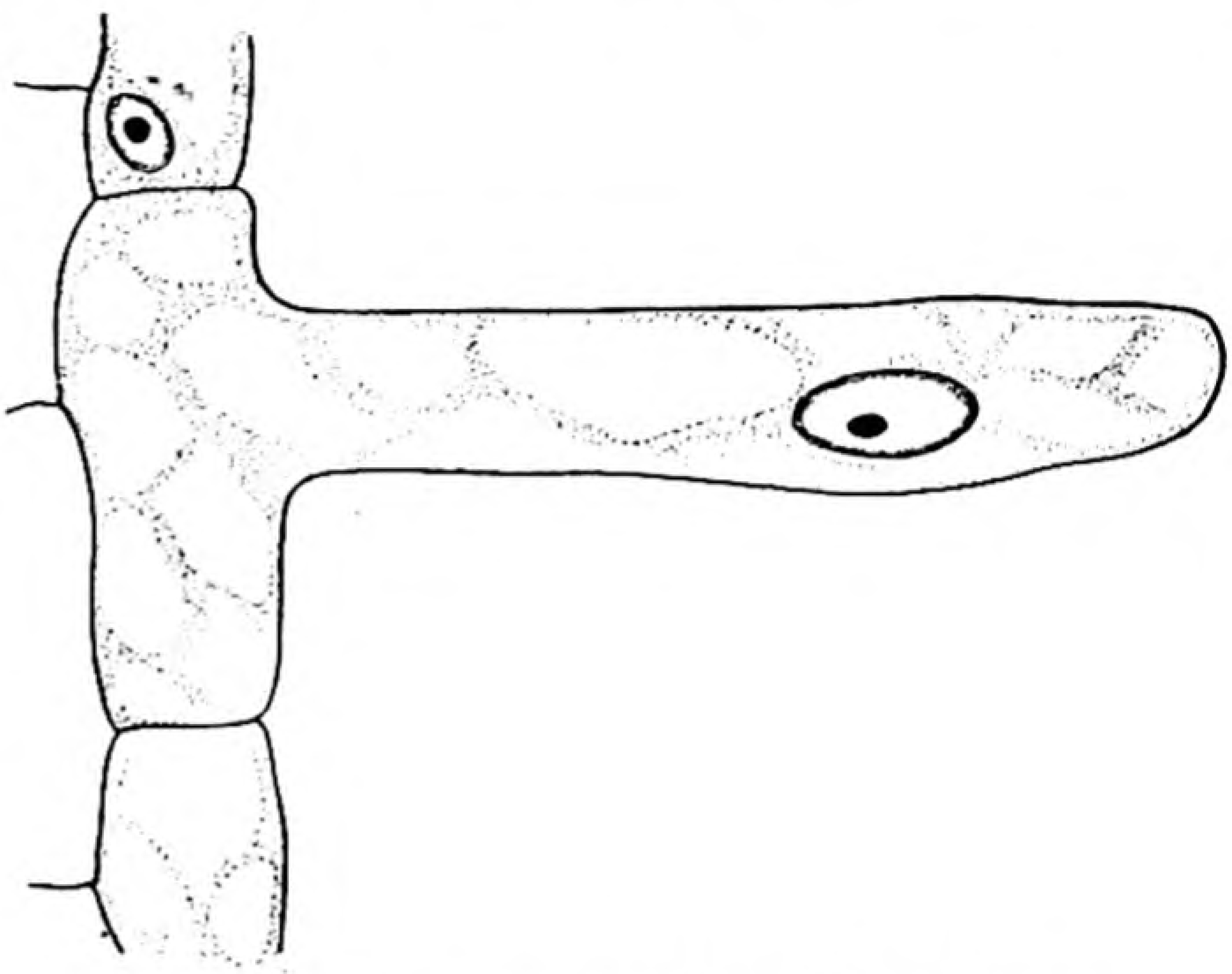


Diagram illustrating behavior of molecules in osmoscope under two conditions. Smaller circles (water molecules) diffuse freely through semipermeable membrane; larger dotted circles (sugar molecules) go through only rarely. (*Left*) Water, following the laws of diffusion, enters from outside; (*right*) following same laws, moves outward through the membrane. A difference in concentration or level always results.

If the membrane with its contents should be placed in a vessel containing a still greater concentration of sugar and with a resulting lower percentage of water than is contained inside, the water would reverse its direction of travel and enough would leave the diffusion shell to equalize the concentration on the two sides of the membrane.

If a diffusion shell filled with the syrup were to be prepared with no outlet tube or other opening and were to be placed in water, enough pressure would develop to burst the membrane, or if it were sufficiently well supported to prevent bursting, a balance would develop between the pressure within and the resistance of the support.

The pressure a given solution is capable of producing if placed in ideal conditions to carry on osmosis is *osmotic pressure*, the stretching of the membrane is *turgor pressure*, and a cell so stretched is said to be *turgid*. Solutions are considered to have high or low osmotic pressure even though they may not be so placed as to exert that pressure. This use of the term means that they could produce pressure if they were placed under suitable conditions. Applying this statement, a concentrated sugar solution has a high osmotic pressure while starch in water has none, because the starch does not dissolve. *The more concentrated the dissolved substance in a solution, the higher the osmotic pressure.* Temperature and concentration, also, have a marked effect on rate and amount of osmotic action. For this reason plants absorb warm water much more rapidly and in greater amounts than cold water. Would warm or cold water be more effective to apply to the roots of a wilted plant?



Root hair. The plasma membrane is semipermeable. Therefore, osmosis takes place.

One other important relationship needs to be dealt with briefly: The higher the concentration of any dissolved substance the lower the freezing point of the solution. Thus, pure water freezes at 0° centigrade, but the addition of salt or sugar prevents freezing until a lower temperature is reached. For this reason some plants are more hardy to cold than others because their cell sap contains larger amounts of sugar, minerals, or other materials that increase osmotic pressure. Their protoplasm, therefore, does not freeze so readily. In fields, some parts of which are well supplied with fertilizers while other parts are not, a frost sometimes damages the crops where the soil is poor while leaving unharmed the plants rooted in enriched ground.

Osmosis and Absorption. The cell is a closed osmotic system. A microscopic examination of a root hair, which is the plant's most effective organ

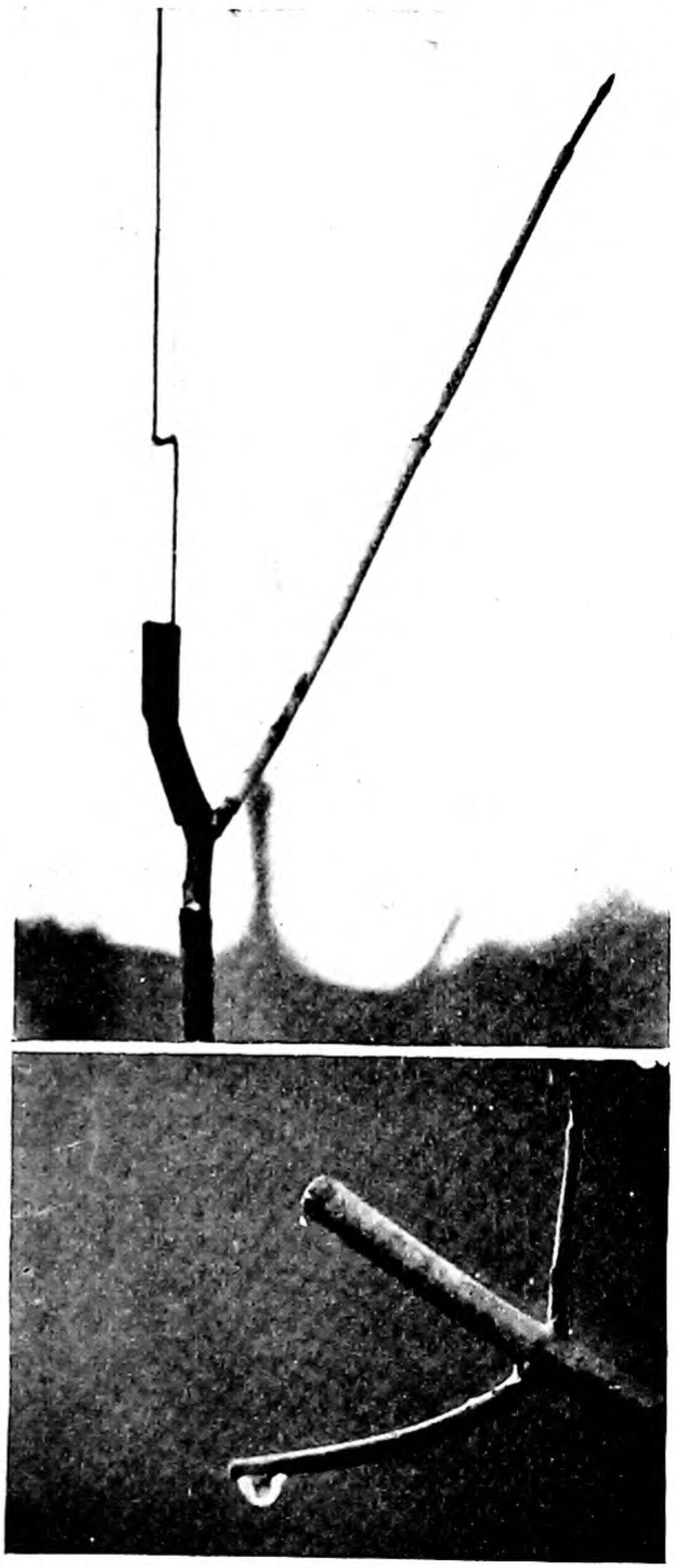
of absorption, shows it to be a long, slender, thin-walled cell whose cytoplasm is distributed mostly in a thin layer just inside the wall. The entire interior of the hair is taken up with large vacuoles. A close resemblance will be seen between this and the diffusion shell described above.

Dissolved materials usually constitute only a small fraction of 1 per cent of the soil solution, much more than 99 per cent of the total being water. The cell sap, on the other hand, contains a somewhat smaller percentage of water. Hence, following the laws of diffusion, water enters the plant osmotically. Under normal conditions there is a gradient from the soil to the leaves so that each cell tends to take water from its neighbors nearer to the soil and to give it up to those nearer to the leaves. In addition, the conductive tubes of the xylem greatly facilitate the passage of water toward the leaves.

The cell sap and the soil water are continuous with each other through the semipermeable plasma membrane of the root hair and osmosis therefore produces a pressure on the inside. Osmotic movement of water to all the cells of the root causes a general turgor, creating in the entire root a certain amount of pressure, the so-called *root pressure*. That this pressure is responsible for a part of the rise of sap in a plant is indicated by the fact that water often runs out of a stump when the stem has been cut off. If a suitable plant is cut and a slender glass tube is fitted to the stump by means of a short piece of rubber tubing used as a coupling, the water will sometimes rise several feet in the tube. The flow of sap from a sugar maple tree and the "bleeding" of grape vines, box elders, or cottonwood trees, when they are pruned at certain times of the year, may be explained by root pressure.

Some recent experiments have shown that, under certain conditions, really amazing pressures are developed by living roots, and there is evidence that some type of vital activity may be at work in the process of absorption in addition to the purely physical action of osmosis. Root pressure may yet be found to be responsible for much movement of water in plants, although in Chapter 9 some extremely potent forces of another kind are shown to be at work.

Because of the osmotic absorption of water into all the cells of a plant, they are normally stretched or turgid at all times. Wilting is simply reduced



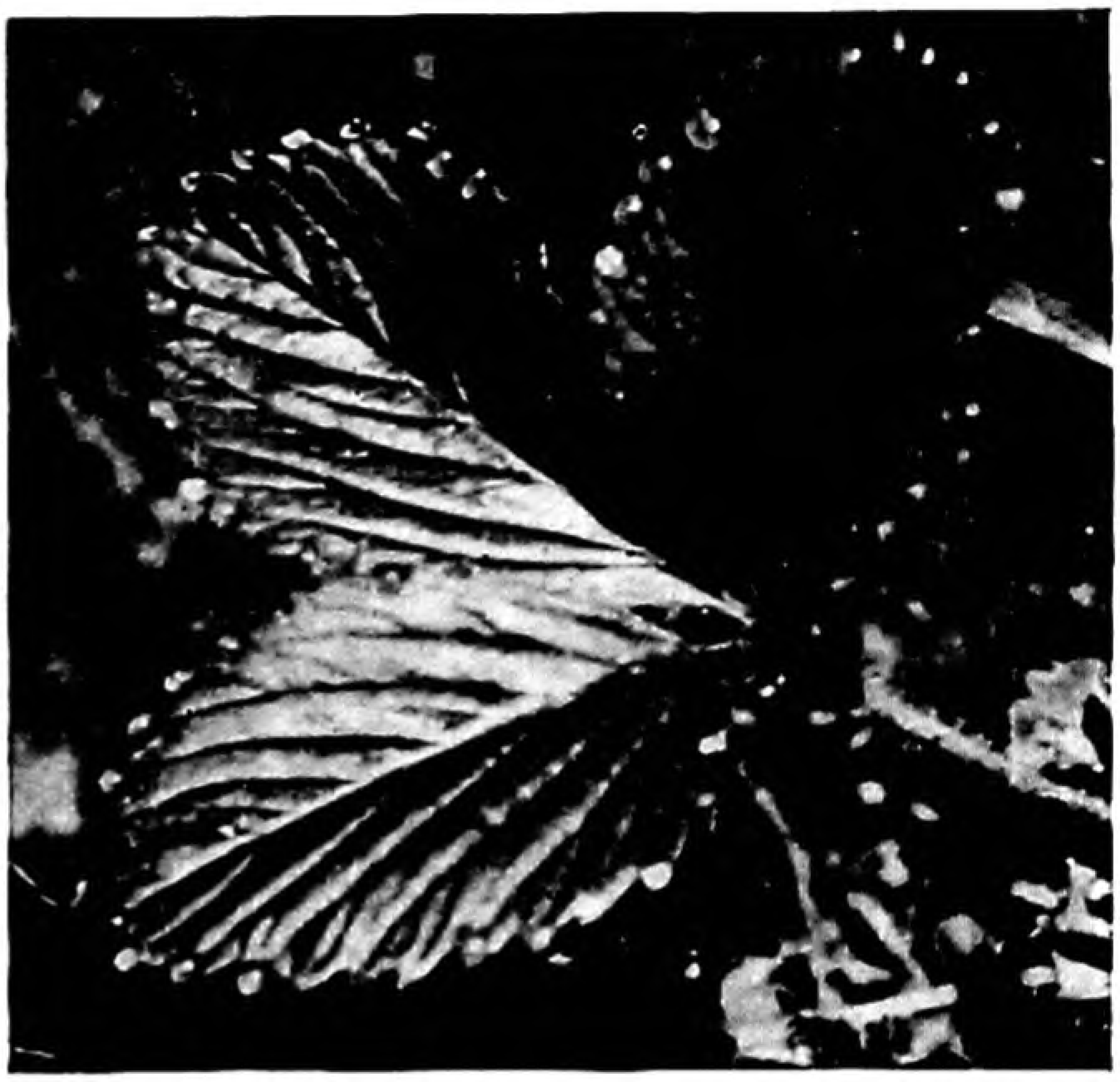
"Bleeding" of box elder twig in early spring. (*Top*) The sap rose to this height in the glass tube in a few minutes. (*Bottom*) One of a series of drops falling from a cut twig of the same tree.

turgor resulting from water loss that exceeds intake. Leaves and younger parts of stems that have not yet developed wood, hold their positions because of turgor, somewhat as an inflated tire holds its shape on account of the stretch produced by air pressure. The tire wilts, so to speak, as soon as the air is released, and in the same way the plant wilts when the turgor in its cells is reduced. In what ways could wilting in plants be brought about? How could turgor be restored to wilted plants? What occurs when plants dry up after a strong salt solution is applied to the roots? In answering the last question students too often say that the salt "poisons" the plant. That this is not the correct explanation can be shown by the fact that a strong solution of such a fertilizer as sodium nitrate will produce similar results. Instead, the explanation should be sought in the application of the laws of diffusion.

The rate or direction traveled by various materials are not necessarily the same for all. Each diffusing substance moves at its own rate from its own greater to its lesser concentration. Thus, if certain minerals are being used by the plant, a deficit results inside and those substances continue to enter. If, on the other hand, other materials are being set free in the cells, these pass outward. In this way dissolved substances enter, while others leave the plant at the same time and place.

Though this explanation accounts for the major part of the exchange of materials between roots and the soil, certain observed facts show that there is some other factor at work. As an example, respiratory activity is linked in some way to the absorption of the inorganic nutrient elements. This connection has been shown in a number of ways. First, some soil nutrients enter cells at concentrations that greatly exceed those which should be expected from simple diffusion. Second, aerobic respiration is required for such specialized intake. This fact has been discovered by reducing the concentration of free oxygen around root tips immersed in nutrient solutions under controlled experimental conditions. Absorption, then, is slowed or stopped in proportion to the available oxygen. Future investigations will, no doubt, find the solution to this situation.

Guttation. When certain kinds of plants, whose roots are well supplied with water, are placed in an atmosphere so moist that transpiration cannot occur, drops of water often appear at the ends of veinlets at the tips or along the margins of



Guttation. Drops of water exuding from hydathodes in the leaves of the strawberry.

leaves. This action can be shown experimentally by thoroughly watering such plants as corn or oat seedlings and covering them with a bell jar overnight. This type of water loss is known as *guttation* (*gutta*, a drop). It will be noted that in this case the water leaves the plant in the form of a liquid and not as vapor as occurs in transpiration.

A close examination of the point where the drop is attached will often show a special type of stoma, the *water stoma* or *hydathode*, through which the liquid has escaped. A small mass of glandular tissue, the *epithema*, can sometimes be found at the end of the vein under a hydathode. This gland secretes the water. The water lost by transpiration is, of course, almost pure, since vapor can contain only such other materials as will evaporate with it. That thrown off by guttation, on the other hand, often contains appreciable amounts of mineral substances.

Drops of guttation water can often be seen cling-

ing to the plants of field and lawn early in the morning during summer. In fact much of the so-called "dew" on vegetation consists of water which has been thrown off by guttation from the plants themselves. Dew proper condenses when the temperature becomes so low that the air is saturated with moisture. Dew on plants, therefore, comes from an outside source, while guttation water is given off from the interior of the plant.

Substances, Besides Water, That Are Absorbed. Soil water contains in solution traces of every mineral through which the water flows. Even such substances as gold, silver, or other metals as well as the various constituents of rocks go slightly into solution. Applying the laws of diffusion to the rooted plant, it is easy to predict that any substance in solution in the ground water will enter the plant unless the plasma membrane is impermeable to it. This is exactly what does occur. Even powerful poisons are sometimes absorbed in this way.

In the more arid parts of the United States some of the soils contain considerable amounts of selenium compounds. Selenium is so poisonous that only a few species of plants can tolerate even a small amount of it. Certain ones, however, seem to require it and others can endure without apparent harm some hundreds of parts of this element per million parts of plant tissue. Yet even these sometimes absorb enough to cause their death.

Plants containing selenium seem to be distasteful to native wild animals, but domestic livestock occasionally will eat enough of them to cause serious illness or even death.

Unless a dissolved substance is used in metabolism, it usually enters only sufficiently to produce an equal concentration on the interior and exterior of the root cells. On the other hand, such nutrients as nitrates are absorbed much more rapidly than are minerals that are not essential to the building of protoplasm. Why? If an accurate answer to this question has been found it is clear that the solutes are not merely swept into the plant by the entering water but that each mineral in solution follows its own gradient and enters or leaves the plant independently of every other.

In the growing plant, carbon dioxide is formed continually in the roots, as in all other parts, in the process of respiration. In many cases the concentration of the carbon dioxide in solution in the cell sap becomes greater than that in the soil water outside the plant. In what direction will it travel under these conditions? By what artificial means could this gas be caused to enter roots from the soil?

Summary. Water is necessary in almost all phases of metabolism. It enters the plant by absorption which takes place largely by the process of osmosis. Osmosis, in turn, is diffusion under special conditions.

The growing plant loses very large amounts of water in transpiration. Transpiration is retarded in many plants by an impervious epidermis, by temporary closure of stomata, by wilting, and by other less evident means.

SUPPLEMENTARY READINGS

Curtis, "The Translocation of Solutes in Plants."
Curtis and Clark, "An Introduction to Plant Physiology."
Dixon, "Transpiration and the Ascent of Sap in Plants."
Kramer, "Plants and Soil Water Relations."
Loftfield, "The Behavior of Stomata."
Maksimov, "The Plant in Relation to Water."

Chapter 7

ROOTS AND THEIR FUNCTIONS

The root is primarily a soil-adjusted organ, although in some highly specialized plants it is suspended in air or water.

Roots usually have two chief functions: *anchorage*, i.e., holding the plant in a stationary position, and *absorption* of water and dissolved substances from the soil.

The following outline of the chapter should be of service in the detailed study that is required.

ROOT FORM AND ORGANIZATION

Perhaps 375 million years ago roots did not exist. Geologists have ample evidence that there were many plants then but apparently none were rooted to the ground. In fact all were very simply and slightly organized. With the passing of time some of the ancient inhabitants of shallow swamps began to grow in places somewhat less wet than the habitats of their ancestors. Certain of these pioneers from water into the air and soil appear to have developed the first woody conductive cells that ever existed on earth. Since that time woody plants have gradually migrated into practically every type of locality with the exception of deep water, while their lowly relatives, the algae, have remained almost exclusively in water or in wet places.

These statements are a brief interpretation of the

evidences that have come from the discovery and critical study of ever increasing numbers of early fossils. A fuller account of this subject is given in Chapter 18.

Among those new land plants that developed woody tissues were some with primitive stems that grew under the surface of the soil, here and there sending up leafless or almost leafless shoots into the air and light. Many of these plants appear to have had no structures that could be properly called roots, both the functions of anchorage and of absorption having been performed by the subterranean stems. Then came certain forms with peculiar rootlike branches extending out into the soil from the underground stems. These branches may be interpreted as the forerunners of roots, for relatively soon, geologically speaking, what seem to be closely related plants are known to have been in existence, having definite roots that were distinct from stems. Many of these plants appear to have migrated from the mud into soil that was much drier, becoming mesophytes, although their ancestors had been hydrophytes. That is to say, the more highly organized forms with their specialized conductive tissues (xylem and phloem) were able to live in soil that was not wet but was only moist. This new ability came about because the woody tissue, that is, xylem, was capable of transferring water from the roots in the moist ground and distributing it throughout the photosynthetic tissues in the aerial shoots, and the phloem, presumably, carried the products of photosynthesis into the roots, supplying them with food.

The question may be asked at this point as to how such radical changes in structure and manner of life as have been outlined above could have taken place. It is, of course, impossible to give answers based on direct observation or experimentation. It is known, however, from critical studies of present-day plants that both their structure and their physiology are largely controlled by the genes. There is no evidence that ancient plants were governed in any manner different from modern ones. The observed variations must have come about through a long series of alterations in genes or their combinations, occurring down through the several millions of years in which these plants were slowly becoming established on land. The basis of this belief is the known fact that genetic changes of several kinds occasionally occur in present-day plants.

Since those ancient periods numerous new characteristics have gradually appeared in roots, resulting in the types to be found at the present time.

In order to make accurate interpretations of the activities of roots and the structural features by which these actions are carried on, it should be kept in mind that roots have undergone their evolution as structures imbedded in the soil. Just as the significant facts about leaves are mostly centered around their functions related to air and light, so roots have many features that make possible a high degree of effectiveness in the absorption of water and other substances from the earth, while, at the same time, they hold the plant stationary.

Roots and Stems. On superficial examination roots and stems appear to be very much alike. Because of a failure to distinguish sharply between the two, students often suppose that the chief distinction is that roots grow in soil and stems in air. While this is true in many instances, there are also large numbers of stems of modern plants that grow underground and roots of many kinds of plants that live in the air.

When it is necessary to distinguish between the two, which is often the case in actual practice, the botanist must have some reliable means of deciding whether he is dealing with root or stem. In all but rare instances a single criterion can be used as a means of recognizing the two. It is this: The stem always has nodes and internodes wherever it grows and the root never has them under any circumstances. Nodes are the places on the stem to which leaves are attached. In some underground stems, that is, rhizomes, many of these leaves develop very poorly, taking the form of scales. Nevertheless, their points of attachment have the same opposite or spiral arrangement as that of the leaves of the aerial stems of the same plant. Such specially arranged appendages are absent in roots.

Examination of underground structures or of aerial ones which might be roots should begin with a search for evenly spaced structures, large or small, which could be interpreted as leaves, or for buds so arranged that they might be in the axillary position.

If a spiral or opposite arrangement is found, similar to that of leaves on an aerial shoot, the structure in hand is almost certainly a stem; if wanting, it is probably a root.

Idealized drawing of end of root as seen with low magnification.

In ordinary upright plants there is, at or near the surface of the ground, a more or less extended transitional zone of tissue that is of neither typical root nor typical stem structure. In the young seedling this part is in the vicinity of the seed, where the root and shoot grow in opposite directions, the one growing down into the soil and the other up into the air.

External Features of Young Roots. Young roots attached to the soil adhere to it so firmly that they are likely to be damaged when they are removed. For this reason the best material for study can be obtained by germinating seeds under such conditions that their roots grow in moist air.

When development takes place under these conditions, a thimblelike covering of the end of the root, the *root cap*, may often be detected by means of a small degree of magnification. In some kinds of plants this structure is conspicuous, but in others it is difficult to see except in specially prepared longitudinal sections of the root tip. The root cap may be regarded as a protective coating which shields the tender underlying tissues from injury as the root elongates and the tip is pushed into the soil.

Just behind the root cap is a tender region of active growth, the *apical meristem*, in which mitotic division takes place very rapidly. On its outer surface, that is, the surface in contact with the root cap, the apical meristem produces the young inner cells of that structure. On the opposite side the developing meristematic cells become longer, increasing the length of the root.

Young root of sunflower marked at 5 mm. intervals with India ink and allowed to grow, to show location of region of elongation. Almost all the growth occurred in the 10 mm. nearest the root tip.

The place and rate of elongation may be determined in the laboratory by making a series of marks with India ink at equal intervals on the younger parts of roots and observing the increase in distance between them as growth continues. By this means it becomes evident that the most rapid extension takes place a short distance behind the apical meristem. This part is called the *region of elongation.* It is responsible for the prolongation of the root tip into the soil. There is gradually less increase farther away from the apex until a region is reached in which there is no further growth in length. This is the region of *mature* or *permanent tissues.*

Just behind the region of elongation the young mature root develops a covering of fine white hairs, the *root hairs.* When in the ground these become firmly attached to the soil particles. What would become of them if they were to be formed in the region of elongation?

Root hairs of corn seedling firmly attached to soil particles.

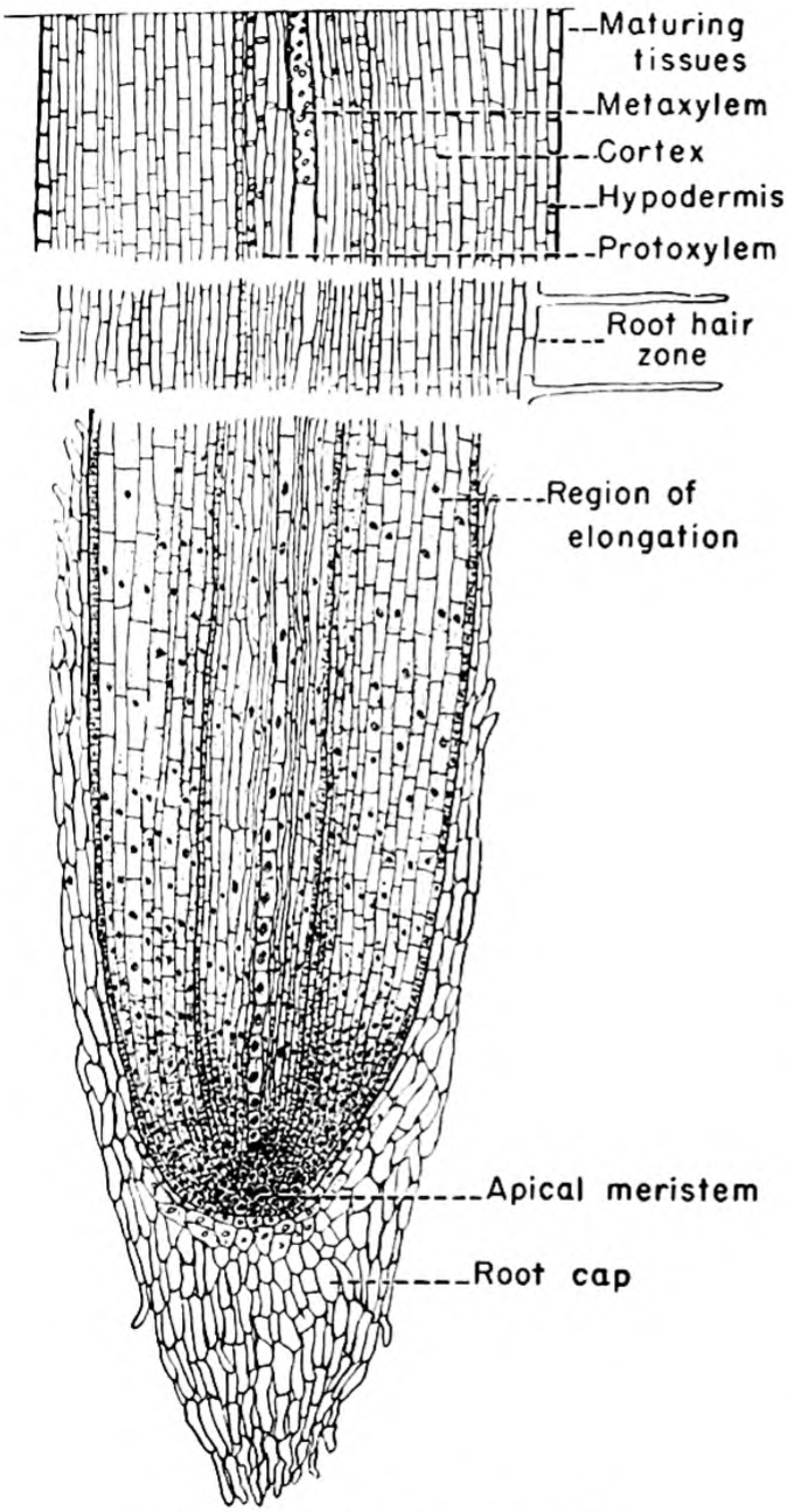
The root hairs are responsible for most of the absorption of materials from the soil. Each consists of a single epidermal cell which has extended at right angles to the surface of the root. Any young cell of the epidermis of a root can absorb water and dissolved substances, but the amount of surface which it has in contact with the soil is so small that its capacity for absorption is limited. If it elongates into a root hair, it has many times as much surface as if it remained unchanged. Root hairs are usually very numerous. Estimates made from careful counts indicate that there may be as many as 1,900 on one millimeter of length of a corn root. Measurements show that a root well supplied with them may have from five to eighteen times as much absorbing area as if it were free of hairs.

The older root hairs die after a time, thus limiting the width of the zone of active absorption. Since new ones are continually forming toward the tip of the root and the older ones are dying farther back, the zone of active hairs on each rootlet moves slowly forward as the root grows, continually bringing the most effective absorbing surfaces into contact with new soil.

Internal Structure of the Root. ORGANIZATION. A longitudinal section cut through the tip of a root usually shows the nature of the cap more clearly than it can be seen from the outside. The innermost cells of the cap are small and compact while those on the outside are larger and are loosely attached to each other. The root cap grows from the inside and its old collapsing outer cells wear off as it is pushed through the soil. By this means the tender apical meristem immediately behind the cap is protected from damage. It is in the apical meristem that the most active division of cells takes place. This tissue can be recognized by the dense protoplasm and relatively large nuclei of the small cells. Behind it lies the region of elongation. Here the cells gradually become longer and the protoplasm has correspondingly larger vacuoles than in the apical meristem. Beyond this region the internal tissues are beginning to differentiate and mature.

Most other important features of internal

anatomy of the root are shown in a cross section made a little behind the region of elongation, where the meristematic tissues have been replaced by mature structures. If the root hairs are still alive at



Longitudinal section of root tip.

this point, the epidermis will still be in good condition; but so many of the epidermal cells develop into root hairs that when the hairs die, the epidermis disintegrates. Following the death of the epidermis, a few layers of the cells just inside undergo changes which cause them to form a waterproof layer, the *hypodermis*, which, from this time on, greatly reduces both absorption and loss of water. Still later a layer of cork may be developed as a permanent waterproof protective coat, but a full discussion of this point will be omitted for the present. (See p. 76.)

A superficial examination of the transverse section of a root young enough still to have epidermis shows that, besides that layer, there are two distinct parts, the central *stele* and the surrounding *cortex*. The row of cells which clearly marks the boundary between these two parts is the *endodermis*. It is to be regarded as the innermost layer of the cortex.

The portion of the root outside the endodermis may frequently contain considerable amounts of stored food. Otherwise the cortex plays no very important part in the activity of the root except during the time when the root hairs are still alive. In older roots cortical cells become variously modified or gradually die from the outside inward.

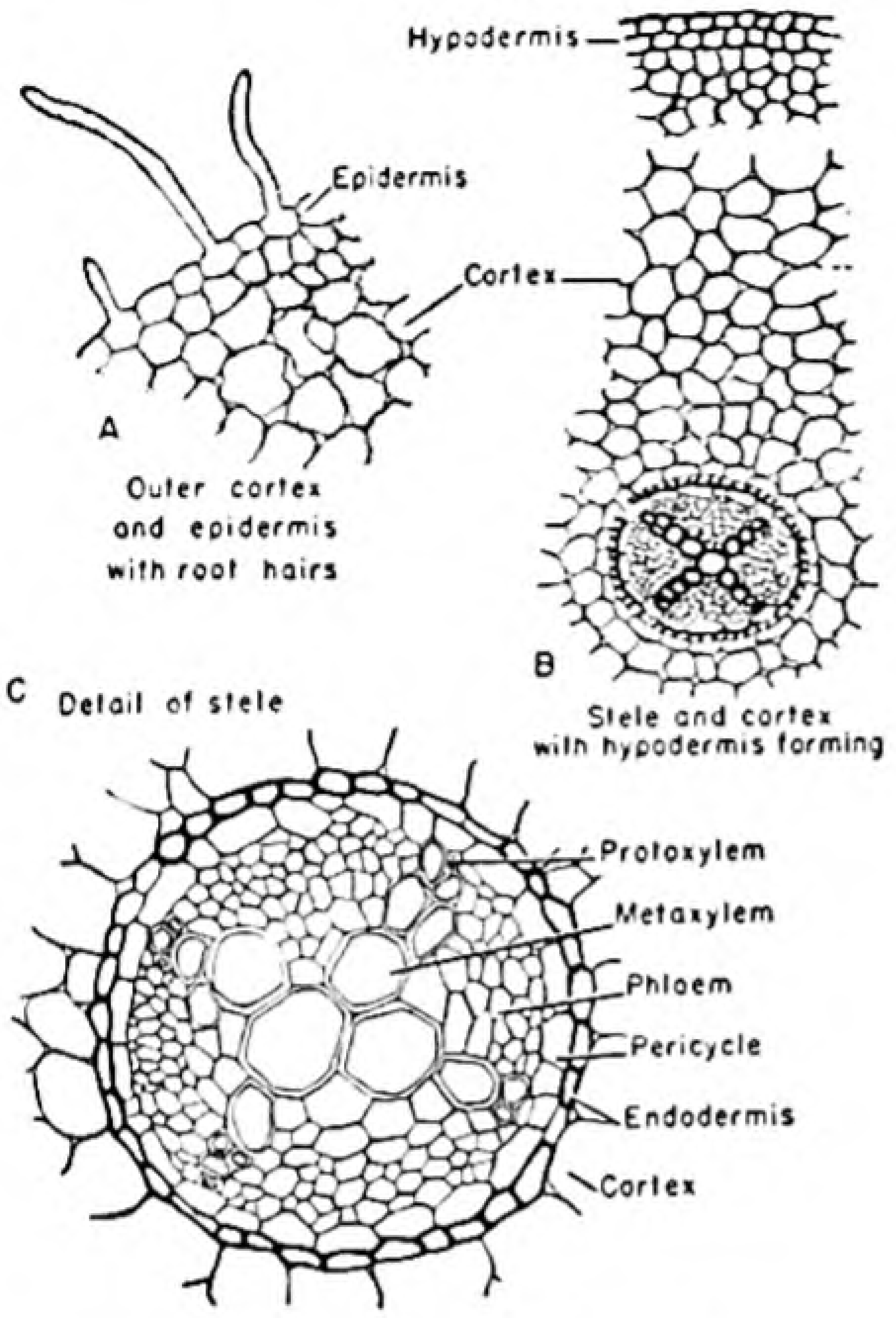
THE STELE. The stele is made up of xylem, phloem, and pericycle. The xylem and phloem carry water and food, respectively, and are continuous from the roots, throughout the stem, and to the ultimate endings of the veinlets of the leaves, making an unbroken conductive channel throughout the length of the plant. Together, the xylem and phloem are often called the *vascular tissues* (*vas*, a vessel) because they are constructed largely of conductive vessels.

The pericycle forms the outermost layer or zone of cells of the stele. On its outer side it is attached to the cells of the endodermis, which constitutes the inner boundary of the cortex.

The stele varies greatly in appearance in different roots, but all forms can be reduced to a single pattern. The appearance of roots of different sizes from the same plant is more confusing than that of the roots of the same size from different kinds of plants.

As a rule, the most prominent part of the stele is the *xylem*, the tissue which carries water. It is made up chiefly of large, rounded, thick-walled tubes.

Cross sections of small roots (these being easiest to understand) show that the xylem cells are often arranged in a star-shaped design occupying the central part of the stele. The star may have various



Cross sections of roots.

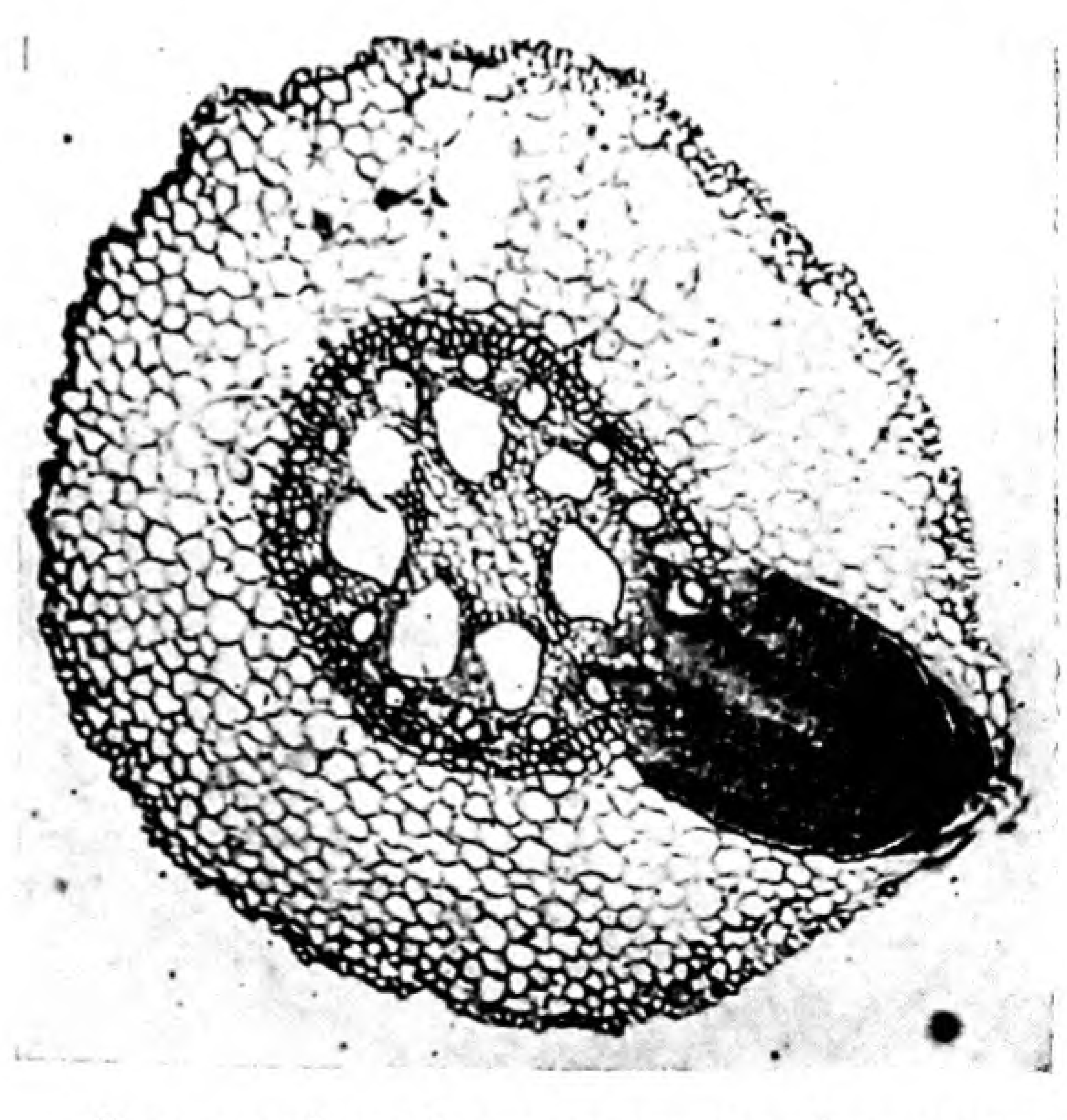
numbers of points, from a large number in some species to only one or two in others. In case of the latter a little imagination must be exercised to call the figure a star. As the root matures and differentiates behind the growing tip, the first cells of the xylem to be formed are the small ones at the points of the star, and development proceeds from these points inward. The portion of the xylem which matures while that part of the root is still elongating is known as *protoxylem* (*protos*, first). Protoxylem cells can often be distinguished by the fact that they are usually definitely smaller in diameter than those of the *metaxylem* (*meta*, after), which is the part that matures after elongation of that section of the root has ceased.

Areas of *phloem*—the tissue which carries food—lie between the points of the star of xylem. The phloem is sometimes difficult to recognize and for the present it is necessary to recognize it by location only.

Outside the xylem and phloem and just inside the layer of endodermis is the *pericycle*. This tissue varies in appearance from root to root but it has one constant important characteristic: It is the portion of the root in which further growth can take place and from which branches arise. In other words, it is a meristem.

ORIGIN OF BRANCHES. Root branches originate in the pericycle opposite the points of protoxylem. Their development begins with a period of active cell division and the formation of an apical meristem similar to that of the main root. This meristem breaks through the endodermis and grows outward, digesting its way through the cortex as it goes. In a short time the tissues differentiate in exactly the same way as those from any apical meristem of a root. Since the branches originate opposite the points of xylem, they naturally fall in rows extending along the root as seen from the outside. By carefully counting the rows of root branches, therefore, it is usually possible to determine the number of points of the star of xylem as seen in cross section. As it extends into the soil every normal branch develops a zone of root hairs, in this way increasing the absorptive surface of the root system.

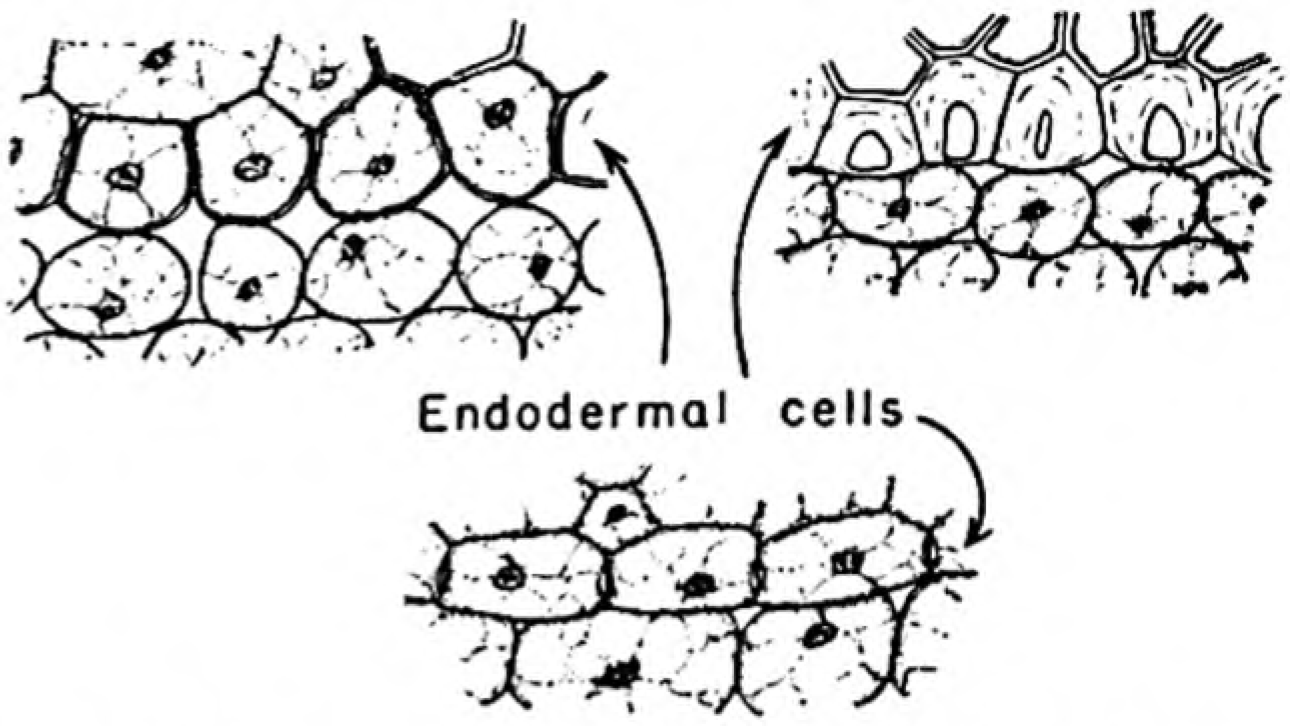
THE ENDODERMIS. The endodermis, that peculiar inner layer of the cortex, presents some problems which have not yet been completely solved. Its



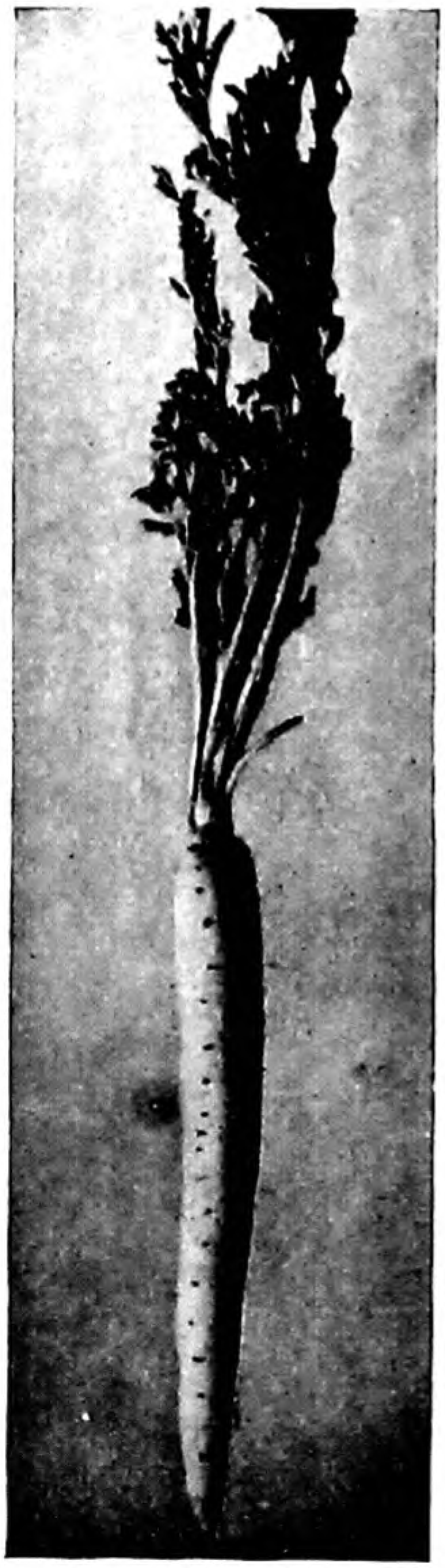
Cross section of corn root, showing young branch developing from pericycle and digesting its way through the cortex.

function is not definitely known, but its peculiar structure in many plants suggests strongly that it probably has uses. It consists of a single layer of cells. In some plants these have all their walls or only their inner ones strongly thickened. In a cross section of a root this chain of thick-walled cells is often very conspicuous. Sometimes additional thickenings are developed in peculiar patterns and at other times the walls are not obviously specialized. In many instances the cells of the endodermis contain heavy deposits of starch, although adjacent cells have none, and for this reason the endodermis is often referred to as the *starch sheath*.

Since walls of the endodermal cells are frequently reinforced with *suberin*, the fatty, waterproof substance which is present in cork, some botanists have thought that the endodermis was important in forming a water-tight sheath around the vascular tissue, in this way preventing the loss of water from the stele. The fact that this tissue is better developed in roots of plants that grow in wet places than in those of dry habitats makes this theory seem doubtful. Others have supposed that the endodermis protects the inner living cells from drowning in excess water.



Endodermis of roots. (*Top, left*) Willow. (*Top, right*) Smilax. (*Bottom*) Buttercup.

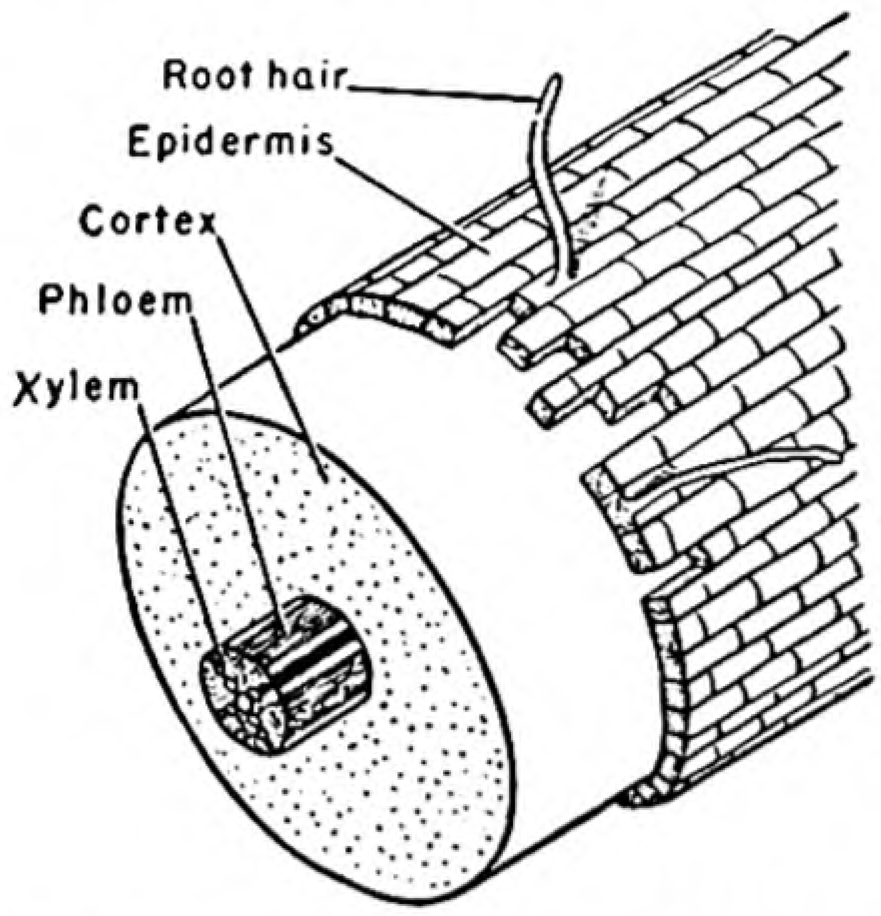


Root of carrot, showing vertical rows of root branches.

Again, the fact that certain cells of the endodermis, the *transfusion cells* or *passage cells*, that form opposite the ends of the rays of xylem do not have the suberized thickenings on their walls, has led to two additional theories. One of these is that the transfusion cells permit water to enter only at the points nearest the xylem while the suberized portion of the endodermis protects the phloem from excess water. The other theory is that the transfusion cells are especially valuable as weak places through which root branches may break. As yet there is not enough evidence to prove certainly the function of either the thick-walled endodermis cells or of the thin-walled transfusion cells.

THE ROOT-TIP AS A UNIT. The foregoing discussion of the internal organization of a root is based on studies made from thin sections cut in various directions and at different places, because that is the only way by which to become acquainted with these structures by means of a microscope. For a

well-rounded understanding, however, it is necessary to visualize the root as a solid in three dimensions. The easiest way to accomplish this is by trying to imagine what each part would be like if all



Diagrammatic, three-dimensional drawing of young root.

the others were cut away. As an aid to such an understanding the relations of the different parts are shown diagrammatically in the illustration above.

The preceding paragraph is based upon study of a young root of small diameter belonging to a dicotyledon. The root of a monocotyledon usually has a much larger number of xylem points, and the differentiated thick-walled xylem cells may not extend all the way to the middle of the root, leaving a pithlike center. (See photomicrograph, p. 83.)

Secondary Thickening. The roots which thus far have been described are relatively small in diameter, and no way has been indicated by which they can grow larger. Many plants, especially those belonging to the pteridophytes and monocotyledons, including ferns, lilies, onions, palm trees, and grasses, never develop any mechanism by which their roots increase in size after they have become mature. Therefore, the roots of such plants always remain slender and uniform in diameter. These are known as *fibrous roots.* Other plants, as for example, common trees, have roots which continue to grow in diameter as long as the tree lives, often attaining very great size.

CAMBIUM. While it is young, a root which has the capacity to increase in size is, in both appearance and structure, exactly like any other small root, except that it organizes between its xylem and phloem, or possibly all over the outside of its xylem, a layer of meristematic cells, the *cambium.* When the remainder of the stele has become well differentiated, the cells of the cambium begin a process of mitotic division which builds up a layer of new tissues extending around the core of xylem and inside the phloem and pericycle. In a short time the inner part of this new tissue begins to develop into xylem, and the outer part into phloem. The new xylem and phloem produced by the cambium are known as *secondary xylem* and *secondary phloem*, as contrasted with the primary tissues which differentiate from the cells left by the growing tip as it moves along.

As the cambium continues to build new cells, the grooves in the original core of primary xylem become more or less filled with secondary xylem, and the isolated areas of phloem tend to run together to form a complete circle outside the cambium.

The development of these new structures deep in the root requires space and produces pressure, causing all parts outside the cambium either to stretch

Origin of cambium in young root.

or to break. The phloem, being still alive at least on its inner surface, remains intact and grows with the enlargement of the more deep-seated parts, but the pericycle, endodermis, and cortex are crushed

and torn until they play no further part in the activity of the root.

THE PERIDERM. At about this time a meristematic layer organizes from the living cells of the pericycle or occasionally in some other part of the living tissues of the root, becoming a *cork cambium*. This cambium produces layers of cork on its outer surface. By stretching as the root grows in diameter, and by building new cork on its outer side as the older parts on the surface of the roots are broken and worn away, this layer provides an effective waterproof covering which continually fits itself to the increasing size of the root and keeps itself in repair. This protective layer is known as the *periderm*.

ROOT FUNCTION

Importance of Anchorage. The roots of most plants that grow tall and upright, firmly anchor the lower end of the stem, holding it in an erect position.

The growing root forces its way through the ground by pushing the soil particles aside and packing them more firmly against each other. In the case of most of the larger woody plants, such as the more characteristic trees, the roots grow in diameter, year by year, in this way maintaining a firm pressure against the soil. The resulting friction and anchoring effects are greatly enhanced by the root branches that extend at various angles in all directions.

Younger and smaller plants are very effectively attached to the soil by the root hairs. As individuals these hairs are almost unbelievably delicate, but the roots of even a young seedling may often have hundreds of thousands or even millions of them. They not only wedge themselves into the minute spaces between the particles, but the cellulose walls themselves are covered by pectic substances, effectively gluing each hair to all solids which it touches. The total holding effects are so great that the stem is likely to be broken off or considerable quantities of soil brought up if an attempt is made to pull such plants from the ground (see cut on p. 81).

When a heavy wind storm sweeps over a forest made up of many kinds of trees, certain species are much more likely to be uprooted than others. On close examination the fallen trees are usually found to have their entire root systems extending horizontally rather near the surface of the soil. On the other hand, those trees with strong, deep roots extending downward in a more or less vertical direction more often either withstand the storm or break above the surface of the ground, leaving the roots unmoved. A tree that has been uprooted by the wind or some other such agency is usually greatly handicapped in further growth and development, even though it still has enough roots in the soil to absorb sufficient water and minerals, because the leaves are not efficiently placed in the light and air.

Balance between Absorption and Transpiration. The fact was stressed in Chapter 6 that water and dissolved minerals enter the root tips by a special form of diffusion called osmosis. Under usual conditions the relationships between the roots and soil on the one hand and the roots and the leafy shoot on the other remain rather constant.

It is chiefly at times when normal functioning of some part of the absorptive or conductive system of the plant is disrupted that the importance of a balance between intake and outgo becomes evident.

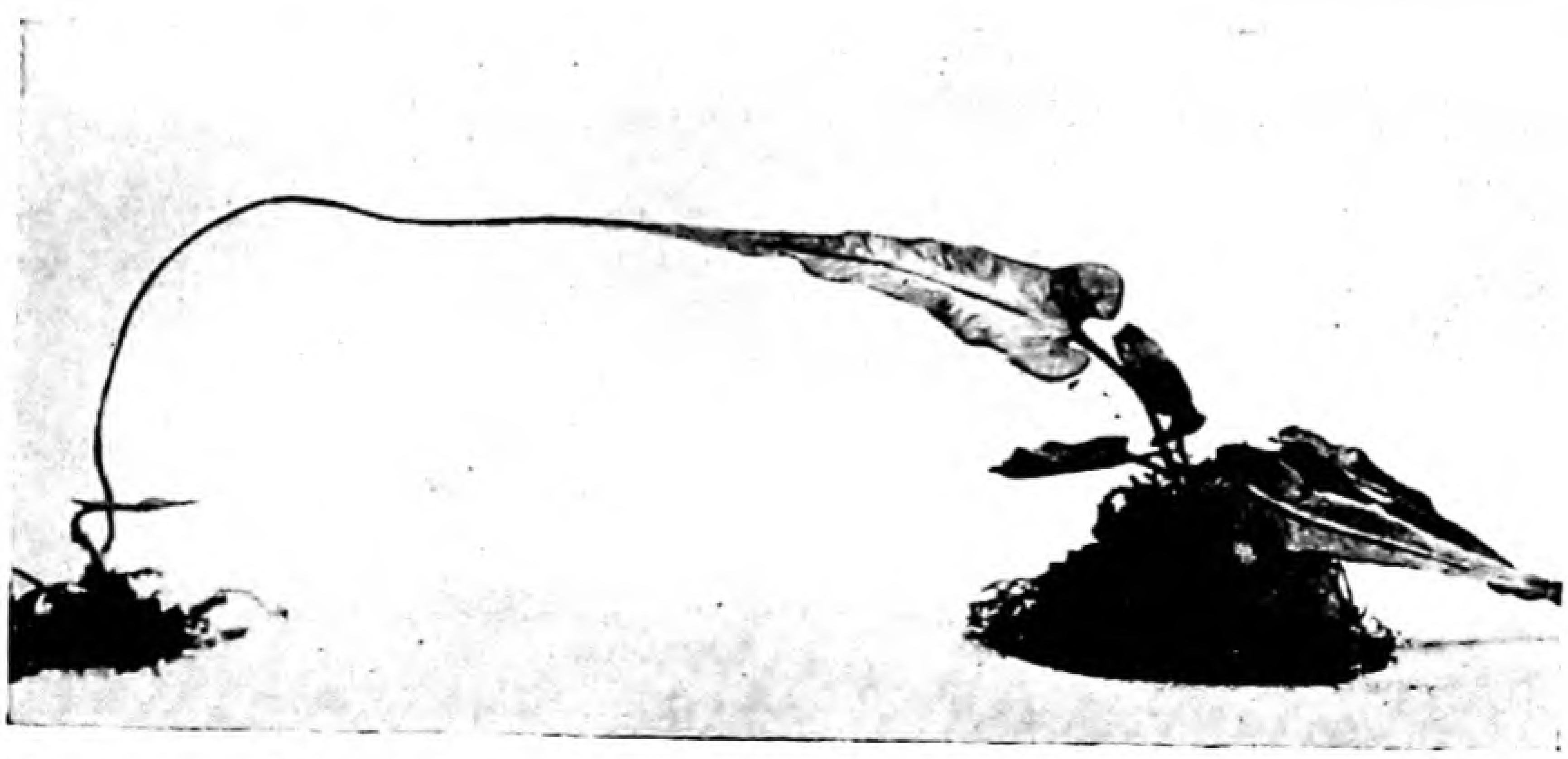
As an example, in resetting plants, even with the greatest care, many of the root tips and root hairs are damaged or destroyed. Wilting almost always results, because transpiration continues while absorption is checked.

If many of the leaves are removed before the plant is taken from the soil or if protection from transpiration is given in some other way, wilting is not so severe, and within a few days new root branches are likely to form with their numberless root hairs. Soon the absorbing structure becomes sufficiently effective to supply water again as rapidly as it is needed. If, on the other hand, such precautions are not taken, the plant may dry up and die before it can reëstablish its connections with the soil.

In nursery practice young trees are often "root pruned" in some way. Various means are used by which to cut the roots that extend too far to permit the trees to be transplanted easily, without disturbing those that are not too extensive. The plants

are then allowed to grow for some time. This treatment causes the cut roots to branch profusely near the main part of the plant, thus keeping the absorbing organs concentrated in a small volume of earth and making it possible to transplant shrubs and young trees without greatly disturbing their root systems. Without some such preparation few trees could be taken from the nurseries and reset successfully. With this explanation it is easy to see why there are many failures when untreated trees are removed from the woods to home grounds.

Proper root pruning a few months previous to transplanting, a reduction of the amount of transpiring surface by the removal of a considerable



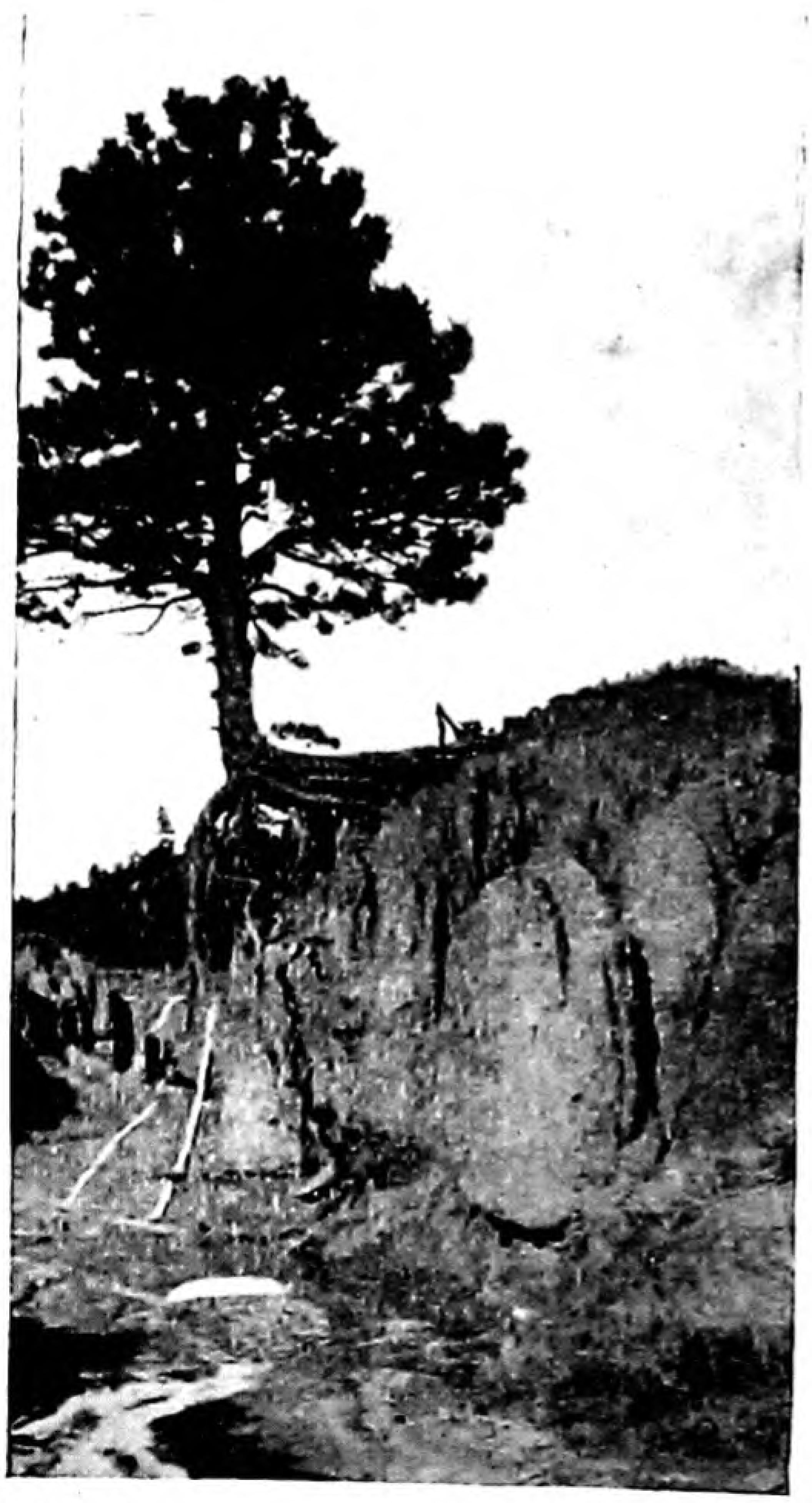
Adventitious roots. (*Top, left*) Brace roots arising adventitiously from node of corn stalk. In the lower part of this photograph, most of the roots are normal root branches. (*Top, right*) Adventitious roots forming on cut end of leaf of *Sansevieria*. (*Bottom*) Adventitious roots and leaves forming on slender leaf tip of walking fern.

number of leaves or leafy branches when the plant is reset, and protection of the root tips and smaller branches from drying, usually result in success in transplanting.

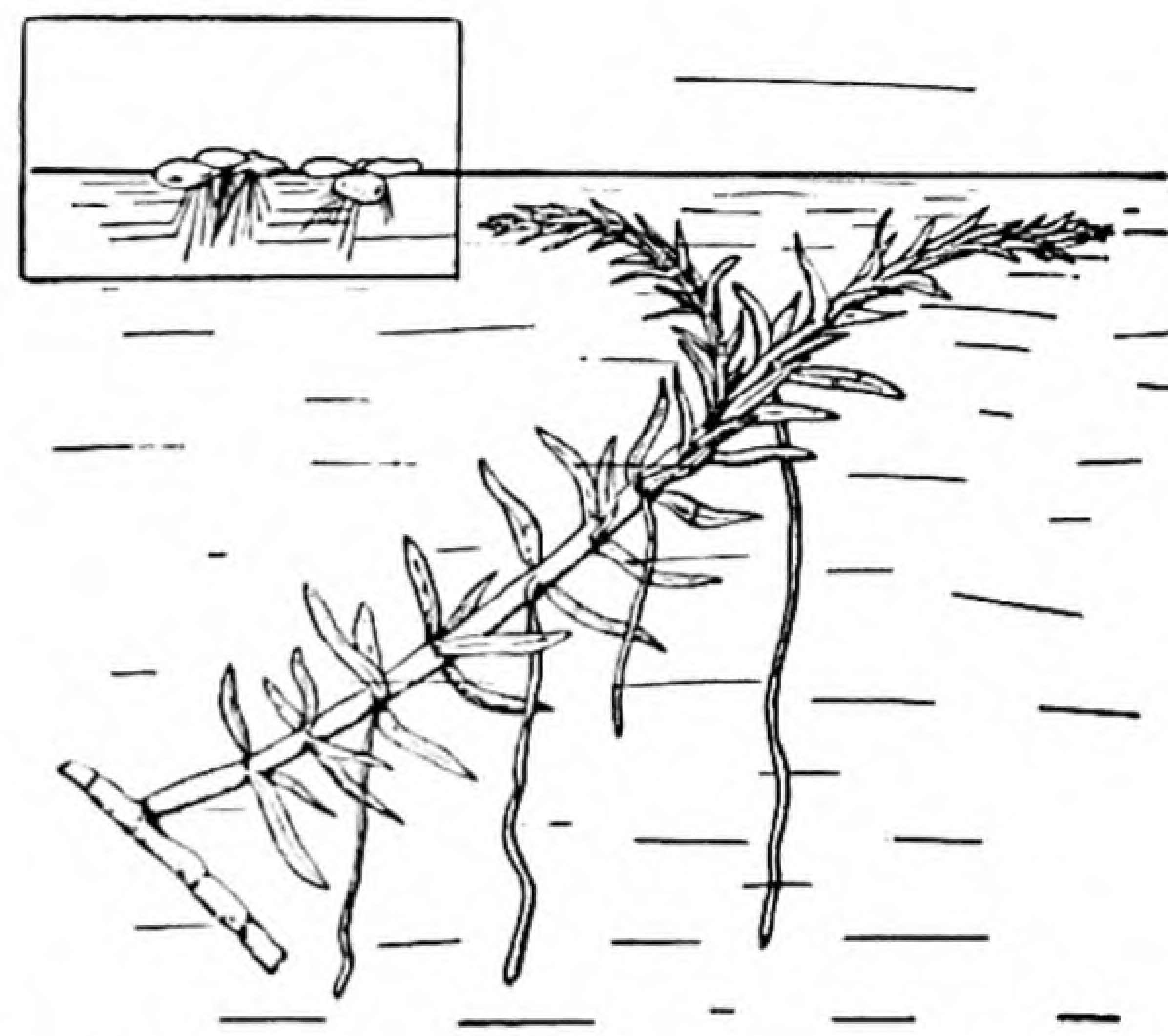
These illustrations emphasize once again the fact that the life of a plant depends on the establishment of a successful balance between the intake and the outgo of water, and to a lesser extent of other materials. This balance is controlled largely by conditions in the soil, in the roots, in the leaves, and in the air. In other words both the plant and its environment are involved.

TYPES OF ROOTS

Different kinds of plants, and even the same kind of plant growing under different conditions, may have roots which vary a great deal in size, appearance, and behavior in the soil, and it is worth while to recognize some of these forms. They may be classified on different bases, and any one root may fit into several classifications, depending upon the basis which is being used.



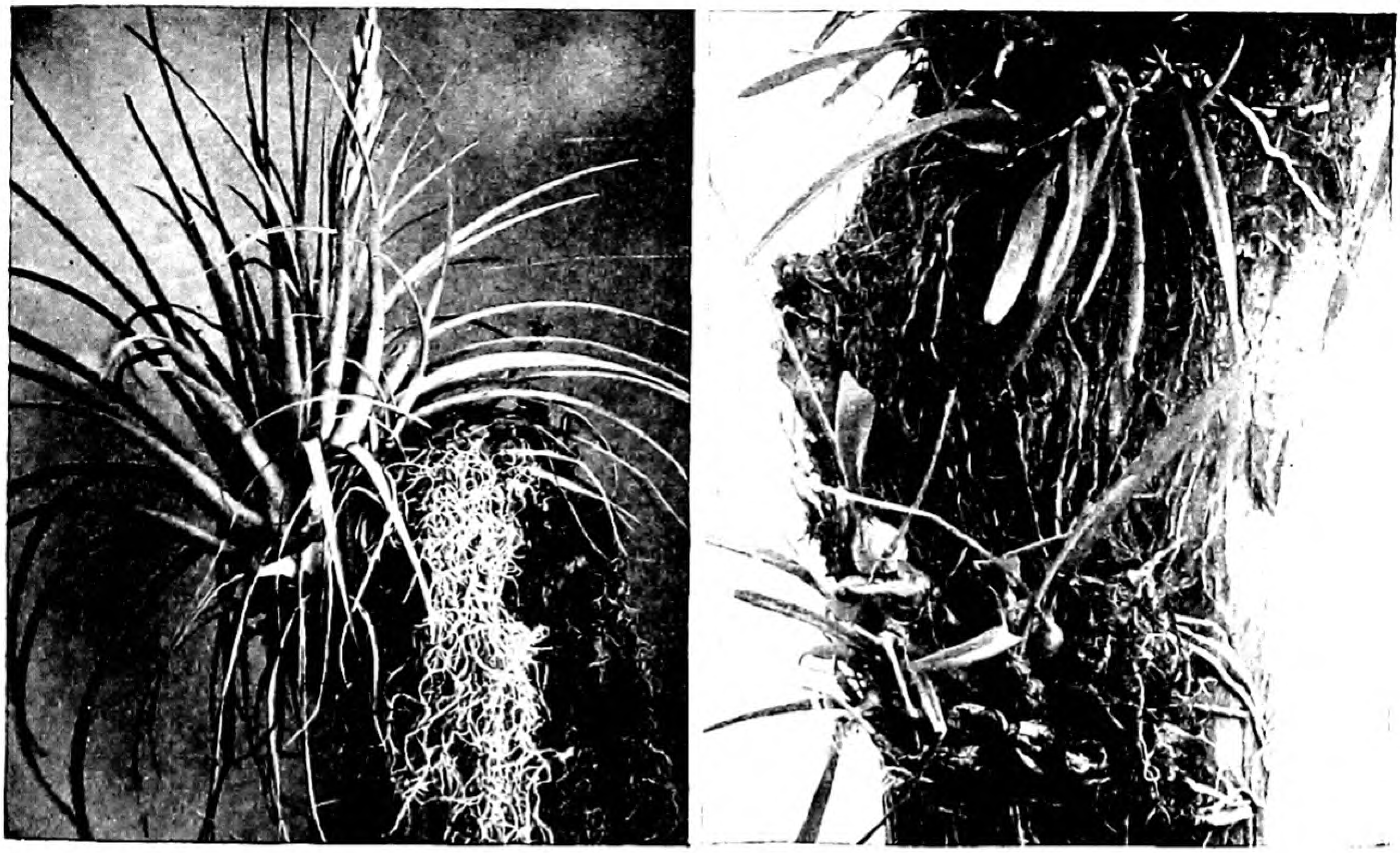
Vertical and horizontal roots of Western Yellow Pine.



Water roots. Large plant, *Elodea*. Small floating plants, *Spirodela*.

Origins. Since roots originate in a number of ways they can be classified according to their origins. A plant embryo in the seed usually has an embryonic root, which is commonly the first structure to elongate into the soil when germination takes place. This first root is called, appropriately, the *primary root*. Those which arise from it are sometimes known as *secondary roots* or simply as *root branches*.

Normal roots arise in only two ways. They may originate in seeds, that is, they may be primary roots, or they may form as branches which are organized in the pericycle of another root. The term, *adventitious roots*, (*adventicius*, foreign, or coming from abroad), applies to those that originate in any other manner. As examples, adventitious roots commonly form on stem cuttings of large numbers of house and greenhouse plants such as geraniums, begonias, coleus, and roses, to mention only a few. By similar means willows and cottonwoods, and sometimes other trees and shrubs, frequently propagate themselves in nature when their twigs fall off



Tropical epiphytes. (*Left*) Two members of the Bromeliaceae. (*Right*) Orchid. Note the roots growing through the dead outer bark of the tree.

and become lodged in mud where they take root. Some of the cacti may establish themselves by similar means even in dry soil.

Likewise, the leaves of a considerable number of plants are capable of giving rise to adventitious roots. For instance, *Sansevieria*, a common ornamental, is propagated by cutting the strap-shaped leaves into pieces a few inches long and standing them up in moist sand. After a few weeks numerous young roots usually organize along the cut surfaces in the sand. Other plants that develop roots from leaf tissues are the walking ferns whose long leaf tips often take root wherever they touch suitable soil, and *Bryophyllum*, *Kalanchoe* and some species of *Begonia* with their meristematic regions in the leaf margins.

One of the most surprising sources of adventitious roots, because so rare, is the fruit of one of the desert cacti of the southwestern United States. This cactus grows upright, forming a somewhat spreading shrub or small tree, on whose branch tips numerous flowers and fruits develop. At maturity the fruits, which are often seedless, fall to the ground, send roots down into the soil and shoots into the air, in this way freely propagating the species.

Relative Sizes. When the primary root grows large, penetrates deep into the soil, and has few or no large branches it is known as a *tap root*. Many garden vegetables such as radishes, turnips, and parsnips have fleshy tap roots. Trees that have well-developed tap roots are especially well equipped to withstand wind storms and to absorb water and dissolved minerals from considerable depths. Many kinds of trees have two sets of roots, a deep, tap root system, and a considerable number of roots that extend horizontally near the surface of the ground. In semiarid regions, where this type is especially common (see photo, p. 88), strong anchorage comes from the combined actions of these two sets. The vertical root holds the trunk upright while the lateral ones, extending far to all sides, act like guy ropes that strongly resist swaying motions occasioned by the wind. Both sets absorb available water very effectively through numerous growing tips.

The roots of many plants, particularly of the grasses, always remain relatively small in diameter, frequently branching very freely with no one dominating the system. These are called *fibrous root systems*. They are especially effective as absorbing organs. Some trees and shrubs with tap roots and large laterals have a subsidiary set of fibrous roots that extend horizontally through the surface soil acting as the "feeders."

Surroundings. Ordinarily, roots grow in soil (soil roots), but those of certain plants grow in water (water roots) and in air (aerial roots). The last are especially common in moist, tropical climates.

Tillandsia usneoides growing on an oak branch.

Some plants that regularly float on water such as the duckweeds (*Spirodela* and *Lemna*) have roots which hang down into the water but do not reach soil. These roots usually are unbranched and do not have root hairs. Other floating plants as, for instance, *Elodea* and *Myriophyllum*, become anchored. Their roots commonly branch and have root hairs only after they reach the mud at the bottom of the water.

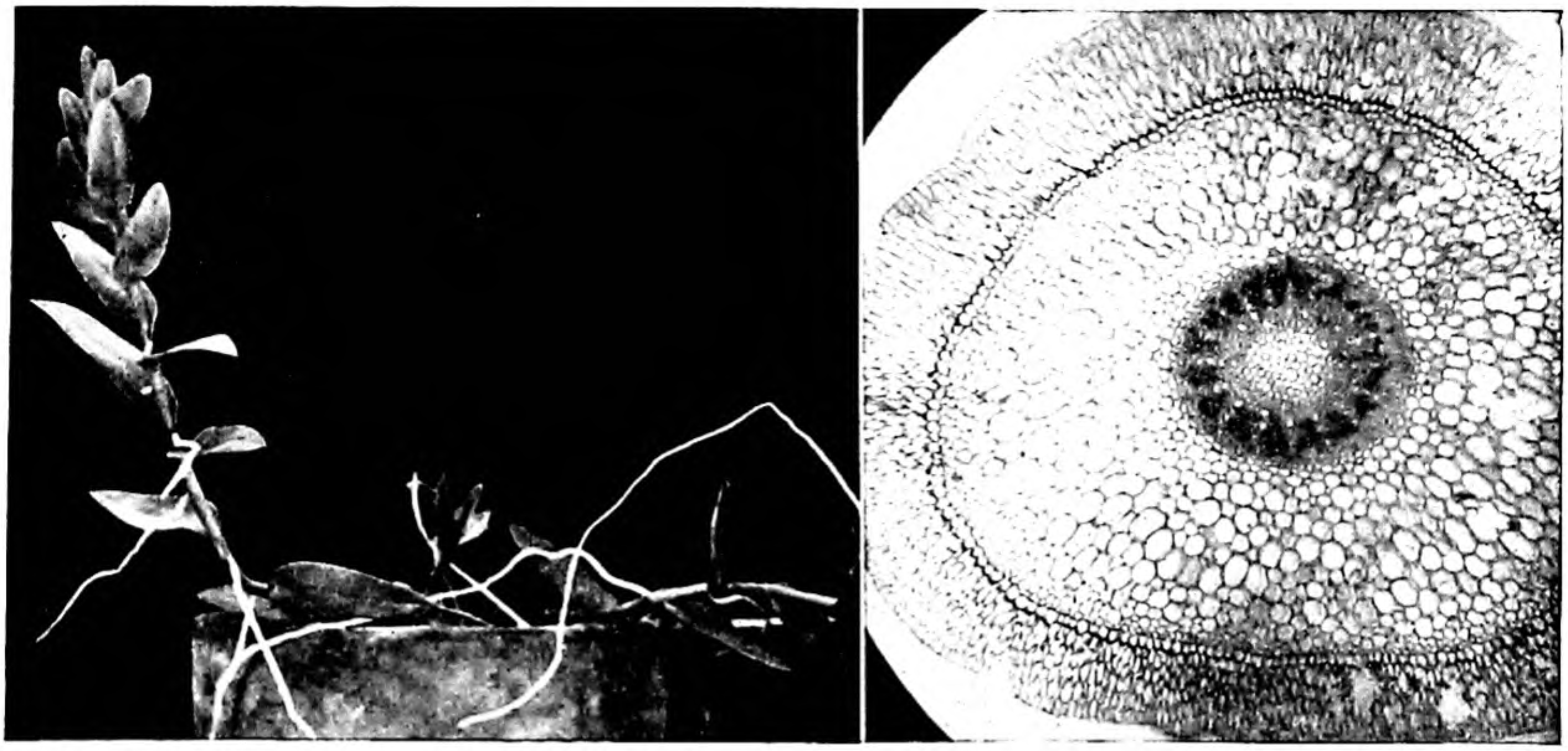
In contrast with these plants that grow with their roots dangling in water are other species that live high on the trunks or even on the leaves of tall trees. Such perched plants are called epiphytes (*epi*, upon; *phyton*, plant). They are especially numerous and highly developed in moist, hot climates, and reach their highest expression in tropical jungles. In these jungles there are epiphytes that represent all the plant groups, thallophytes, bryophytes, pteridophytes, and spermatophytes. Of these, only the last two have roots; therefore thallophytes and bryophytes are not important in this discussion.

The epiphytic pteridophytes and seed plants are represented by large numbers both of species and of individuals in the tropical forests. The majority of the epiphytic pteridophytes are ferns, many of which have highly specialized means of storing and absorbing water.

Epiphytic seed plants are especially numerous in three families. These are the pineapple family (Bromeliaceae), the aroid family (Araceae), and the orchid family (Orchidaceae).

Some of the epiphytic members of the pineapple family have almost the appearance of small pineapple plants growing perched in trees. But the best known member of this family in the United States is the Spanish moss (*Tillandsia usneoides*) of the moist Southeast. In this plant, however, roots scarcely develop, but, instead, absorption takes place through the surfaces of the small leaves and dangling stems, and anchorage can hardly be said to exist.

Like the Bromeliaceae, the aroid family is largely tropical and, therefore, few species are known in the United States. The best known examples of this family are the common wildflower, Jack-in-



(*Left*) Aerial roots of tropical orchid. (*Right*) Photomicrograph of a section showing the velamen, a highly specialized epidermis four or five cells thick, on the surface, followed by a specialized layer, one cell thick, the exodermis. This is the outermost part of the cortex. The cortex, proper, and the parts of the stele are much like those of soil roots.

the-pulpit (*Arisaema triphyllum*) and the cultivated calla. Many of the tropical relatives of these plants grow high up in the forest trees.

Of the wild orchids, probably the ladyslippers are the most universally known in the United States. In the tropical rain forests, besides the ground-inhabiting species, there are large numbers of epiphytic orchids. Some of these are small and unattractive while others are very showy when in flower.

Some of these epiphytes, both ferns and seed plants, develop long roots that finally reach the ground, thus making a normal contact with the soil. The roots of some others spread over and pierce to some extent the loose, decaying outer layer of bark of the tree on which they grow, while those of still others, penetrating more deeply, enter into the living tissues, permitting these plants to live semi-parasitically. The roots of some of these epiphytes merely hang in the wet air, absorbing sufficient amounts of both water and minerals for use in metabolism. In some of the orchids a loose, porous, spongelike coating, called *velamen*, formed of a highly specialized epidermis, absorbs and holds large quantities of water. Dust from the air collects in this tissue and probably provides the necessary minerals.

ROOTS AND THE SOIL

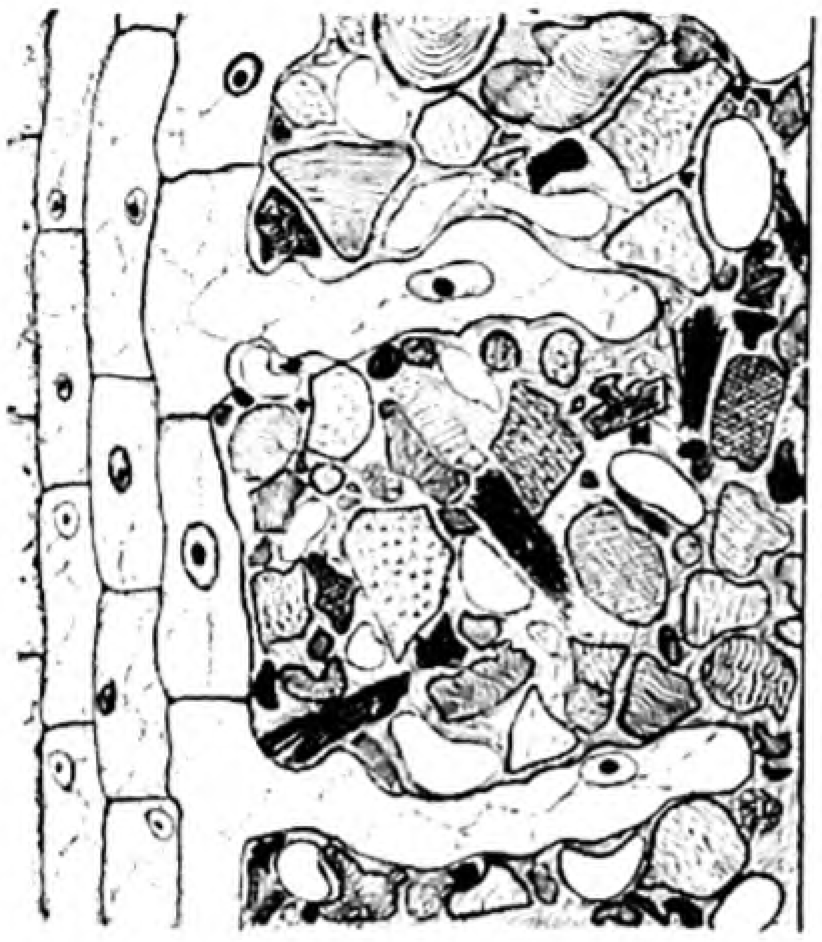
Conditions in the Soil. While roots of some kinds of plants grow in air or water, by far the majority function almost entirely in the soil.

A fertile soil is usually composed of a mixture of sand grains and smaller rock particles of many kinds to which are attached thin layers of gluelike colloidal mixtures. These gelatinous coats are composed of the partly decayed plant and animal refuse that is commonly called humus, countless bacteria of many kinds, including those that play parts in the nitrogen cycle, microscopic animals, and rock particles so small that they are of colloidal size.

If the soil is moist, the colloidal layers are wet with imbibed water; any minerals present are dissolved to a greater or less extent, and moist air fills the intervening spaces, furnishing the oxygen necessary for respiration. Since the soil particles touch each other on various surfaces their films of water are continuous from each one to all its neighbors.

When root hairs grow into the air they extend at right angles to the length of the root, but when they develop in the soil they become very crooked and irregular in shape because they are forced during their growth into the spaces between particles. In

fact, many of the soil particles cling to them so tenaciously that they cannot be removed without breaking the hairs. Such an arrangement brings the root hairs into a relationship with the soil that



Root hairs in soil, showing intimate contacts of soil particles with cell surfaces and with each other.

is ideal for the absorption of water and dissolved minerals.

Mineral Nutrients. This is the story of a small farm in the upper Mississippi Valley. About 125 years ago when early settlers came from the Eastern States to this frontier community, they found the deep, black, rich, moist prairie soil covered by a natural stand of remarkable grasses. Here and there the near monotony of the slightly rolling landscape was relieved by groves of oak and hickory trees.

This individual area which was to become a farm was covered with a dense growth of the great bluejoint grass (*Andropogon furcatus*) which stood tall enough in midsummer to reach a man's shoulders or even in places to overtop his head. With this aristocrat of the prairies there grew scores of species of smaller grasses and of colorful wildflowers, all knit together into a deep, tough sod.

Fine crops of hay could be cut from those prairies and the farm animals were well fed, but hay could not be used for human food. Soon, with great labor, the plow was drawn through the sod, turning up to the sun the black earth with its tangle of underground stems and fibrous roots, completely destroying the age-old plant cover.

Then came a series of years in which corn, potatoes, and other foodstuffs for man and beast were grown with lavish abundance. Half a century passed and the crops were becoming somewhat less successful. The farm was sold and the new owner needed cash for taxes and for general running expenses, and corn was the best money crop. The soil became grayer and less mellow and year by year the number of bushels of corn per acre became fewer and fewer. Although it was obviously unwise, for twenty-five years nothing but corn was planted and this plot of ground came to be known as "the poorest farm in the country." At last it was sold again. The new owner laid careful plans to build the fertility back into the soil. Farm manures were applied liberally and as soon as possible he established a good stand of clover. By these and other means at his command, he had within a few years developed a productive, profitable farm. This story is only one of thousands that illustrate a general situation more or less clearly recognized by the better farmers for many years.

Unknown to these pioneer settlers, two German botanists, Sachs and Knop, were making a scientific attack on the problem of soil fertility at about the same time. The two men developed similar methods of investigation and reached almost identical conclusions. They dissolved measured amounts of inorganic compounds in distilled water and introduced the roots of experimental plants into various combinations of these solutions. Both men finally discovered that plants must have calcium, potassium, nitrogen, sulfur, phosphorus, magnesium, and iron if they are to grow normally. Conversely they found that plants can grow quite well when they are supplied with solutions of compounds containing these elements. Plant physiologists were already fully aware that carbon, hydrogen, and oxygen from water and carbon dioxide are necessary for the production of carbohydrates. Therefore these three with the seven elements named above came to be known as *the ten essential elements* for plant growth. More recently these have come to be called the *major elements*.

Gradually, as more highly refined methods were developed, permitting greater precision in both results and interpretation, it became evident that certain other elements are required in almost unbelievably small amounts. In earlier experiments

these had occurred in the form of accidental contaminants. Even today, with modern advances in manufacturing controls, such contamination occurs continually. The labels on so-called chemically pure (CP) reagents faithfully attest the fact. Only rarely does one find a supply bottle without at least a trace of some foreign substance recorded on the label. In the most exacting work all chemicals must be refined repeatedly to remove unwanted elements, and even with these precautions, the distilled water and glass storage vessels may add measurably to the impurities in a nutrient solution.

The most critical work has shown in recent years that manganese, boron, zinc, copper, and probably molybdenum are required for the normal growth of plants in addition to the ten substances listed above. Therefore, the list of essential elements for the common green plant must now include the following: oxygen, carbon, hydrogen, nitrogen, phosphorus, sulfur, potassium, calcium, magnesium, iron, manganese, boron, zinc, copper and molybdenum. The last five in this list are usually referred to as *minor* or *trace elements*. All fifteen are necessary, but in very different amounts. If any one is absent, the plant is abnormal or may even die. In contrast with the major elements, the minor ones act chiefly as catalysts or as prosthetic portions of enzymes that control various steps in metabolism. These contribute but slightly to the weight of the plant. Such small amounts are required that the zinc coating of a galvanized nail thrust into the soil of a flower pot has been sufficient to correct the zinc deficiency in a potted plant. One part of manganese in ten million parts of culture solution is adequate for some plants. Even one part in ten billion may be sufficient to produce measurable results as compared with complete absence. The following analyses of entire plants and of protoplasm without cell walls gives some clue to the relative weights of the various elements entering into the structure of organisms:

Element	*Symbol*	*Percentage by Weight in Protoplasm*	*Percentage by Weight in Entire Plant*
Oxygen	O	76.	45.
Carbon	C	10.5	44.
Hydrogen	H	10.	6.
Nitrogen	N	2.5	1.5
Phosphorus	P	0.3	0.2
Potassium	K	0.3	1.0
Sulfur	S	0.2	0.2
Iron	Fe	0.01	0.08
Magnesium	Mg	0.02	0.2
Copper	Cu	Trace	..
Boron	B	..	..
Zinc	Zn	Trace	..
Manganese	Mn	Trace	0.04
Molybdenum	Mo	..	..

Water culture methods similar to those used on small scale in laboratory investigations have now been perfected to the point that they are sometimes used for commerical growth of a considerable number of kinds of plants. Giant shallow vats, usually built of concrete, are filled with the proper solutions and the plants are supported in such a way that their roots dip into them. Any one of various methods must always be used to supply oxygen to the roots (See p. 42.). Some device is used to cause air to bubble through the solution or the solution is drained away temporarily to be replaced somewhat later. While prodigious yields have been reported it is doubtful if such culture solutions will soon replace the soil for general use. Nevertheless since such methods are becoming successful, the growth of certain types of crops may soon be almost a factory process requiring the labor of highly trained and skillful botanists and chemists.

Functions of Essential Elements. With the exception of oxygen, probably no element is used by a plant while in the pure form. Even free oxygen probably does not enter into metabolism except in respiration. Then it is lost to the plant because it combines with carbon to form carbon dioxide, which usually diffuses away. What is the source of the oxygen in protoplasm? To be available, all these elements must be combined to form chemical compounds. Thus nitrogen may be utilized in the form of dissolved nitrates, such as sodium nitrate ($NaNO_3$) or potassium nitrate (KNO_3) or it may come from ammonium compounds such as ammonium sulfate ($(NH_4)_2SO_4$) or ammonium nitrate (NH_4NO_3). Sulfur is used in the form of sulfates, such as calcium sulfate ($CaSO_4$).

While each of the essential elements plays its own distinctive part, all must act together in the protoplasm to produce its structure. Thus each affects the total reactions of all the others.

Carbon (C) plays, in a peculiar way, a leading role in all protoplasmic activity, for around its atoms cling the rest of the elements in practically all vital processes. A primary reason why it is the "keystone element" of organic compounds is found in the ability of carbon atoms to unite with one another in complicated groupings, at the same time making chemical union with large numbers of atoms of other elements. The great complexity of protoplasm, which makes possible the extreme degree of variation among living things, is probably due in a very large degree to this unusual property of the carbon atom. Another characteristic of carbon which gives it peculiar significance in organic compounds is its ability to unite readily with oxygen. This makes possible aerobic respiration with its very efficient release of the energy which is necessary in metabolism.

Oxygen (O) is a constituent of carbon dioxide, and by way of the process of photosynthesis, it enters into the structure of all foods and of protoplasm. The story of the energy changes occurring in life processes centers largely around the relationships between oxygen and carbon.

Hydrogen (H) is also indispensable as a constituent of water, of all foods, and of protoplasm.

Nitrogen (N) is an essential part of every protein and, therefore, of protoplasm. Its peculiar significance is discussed in detail in another connection (pp. 59–64). When available to the plant in ample amounts, the foliage is usually green and vigorous because this element is a part of the chlorophyll molecule; when in inadequate amounts, it is yellowish; and when in excess, ripening is retarded.

Potassium (K) plays an important part in cell division and in growth. It also encourages the deposition of starch in tissues. Without it, carbohydrate metabolism is very sluggish, greatly interfering with the health of the plant.

Sulfur (S) enters into the structure of protoplasm and is important in cell division and in the development of fruits.

Phosphorus (P) is a part of the protoplasm, especially of the nuclei. A sufficient supply in the soil is necessary for the ripening of fruits and grains and for root development. Its physiological importance lies largely in the fact that phosphorus enters into many chemical reactions which are necessary in almost all phases of carbohydrate metabolism, even including those final steps in energy release in aerobic respiration.

Calcium (Ca), a constituent of limestone, is used in the formation of calcium pectate, a very important part of cell walls. Without it the cells are loosely fastened together, and the plant suffers accordingly. This element also promotes the growth of roots and leaves and the digestion of starch. In addition, calcium compounds are important in neutralizing the acidity of some soils, thereby improving their texture in such a way as to admit both air and water. When present in proper amounts calcium controls the solubility and therefore the availability of iron, phosphorus, manganese, and some other nutrients.

Magnesium (Mg) is necessary for the production of chlorophyll, because it is a part of the chlorophyll molecule. In addition, it seems to play a part in bringing about the formation of fats.

Iron (Fe) is required in extremely small amounts for the production of chlorophyll, although the chlorophyll molecule does not contain that element. The iron acts as an activator which brings about the formation of chlorophyll.

Manganese (Mn), Zinc (Zn), Copper (Cu), and Iron (Fe) all enter into the structure of the numerous respiratory enzymes. So complex is respiration that each enzyme must carry on its own part of the process before the next can do its work. One is reminded of the conveyor belt in a modern factory where each worker represents an enzyme in the continuous process of producing the final result.

Boron (B) affects translocation and metabolism of the carbohydrates, and in some obscure manner permits the absorption of calcium. Molybdenum (Mo) is important in nitrate metabolism.

Mineral Deficiencies. Slightly more than a century ago (1843) Liebig, the outstanding German chemist of his day, summarized a long series of investigations into plant nutrition and soil chemistry by saying in effect that *the deficiency or absence of one necessary constituent of the soil renders that soil barren even though all other necessities are*

present. He added, "A cropped soil is restored to fertility by adding to it all minerals removed by the plants." These pioneering concepts have come to be called *Liebig's law of the minimum*. We are now coming to realize that this law has much wider application than was at first supposed, applying even to such environmental conditions as light, temperature, and water as well as to soil nutrients.

For centuries experienced farmers have been able to estimate the health of their crops by observing certain characteristics such as color of leaves, rates of growth, and other simple features; but it is only during the last few years that an attempt has been made to organize these observations into a usable body of knowledge. Though there is still much to be accomplished, a measure of success has already been attained. Deficiency of some of the elements causes such definite symptoms that the appearance of the plant will often enable the experienced person to recognize the cause. As an example, nitrogen deficiency results in reduced production of chlorophyll and a pale-green color. Such reduction in the amount of chlorophyll restricts the rate of photosynthesis and hence of growth. The successful gardener or farmer is likely to detect the earliest indication of the loss of the deep-green color of his plants. He now knows that he can correct the condition by the addition of nitrates or ammonium compounds as side dressings in the soil near the root tips. A less frequent but very spectacular deficiency symptom may occur in certain unusual situations. Iron compounds are insoluble and therefore unavailable in certain soils with a strongly alkaline reaction. This condition may result in chlorosis (lack of chlorophyll production) especially between the larger veins of the leaves, while a narrow band along each vein is green. A drop of 1% ferric chloride solution in water placed on the white or yellow part will sometimes cause the production of a bright green spot within a few hours; or a general spraying of the plant may bring about complete recovery.

Air in the Soil. The gardener and the corn or cotton farmer usually believe that their crops grow more vigorously after the soil surface is stirred with hoe or cultivator. These people are probably correct. Living roots are made up of very active tissues. For this reason they usually require considerable amounts of oxygen in their respiration. Stirring the soil introduces greatly increased supplies of air, permitting more rapid aerobic respiration with its highly efficient release of energy. Therefore, all growth processes in the meristematic region are greatly accelerated, and with healthy, vigorous roots effectively absorbing water and nutrient minerals, the entire plant develops rapidly.

The entrance of the gases of the air into ordinary upland soil is aided in large degree by changes in water level. When the ground is filled with water, as after a heavy rain, there is little space left for air, but as the water is removed by drainage, absorption by plants, and evaporation, air comes in to take its place. The next rain again fills the spaces within the soil and drives out the air, making it possible for a new supply to come in as the water drains away again. In this way summer showers alternating with brief dry periods produce a kind of pumping action, alternately driving out stale air and drawing fresh supplies into the layers of soil occupied by all but the deepest roots.

A fertile soil is usually constituted primarily of a mass of non-nutrient and almost insoluble rock derivatives. Important among these are grains of sand and relatively large fragments, ranging in size from gravel to particles too small to be seen without magnification. Associated closely with this matrix are large amounts of clay. Clay is peculiar in that its ultimate particles are of colloidal size, far too small to be seen with even the highest power of the microscope. Chemically, it is aluminum silicate which is variously mixed and combined with numerous other substances. Attractive forces aggregate the submicroscopic particles into granules of various shapes and sizes. As was stated above, a sufficient supply of calcium increases the degree of granulation and therefore improves the texture of the soil by decreasing the tendency of the colloids to cling together into a cementlike mass when they become dry.

In this entire system water plays a peculiar part. When a considerable amount of rain falls, several actions ensue. A large amount is likely to drain downward through such open spaces as there may be between rock fragments, grains of sand, and

granules composed of colloidal clay and humus. This is called *gravitational water*. Commonly it finds its way deep into the soil within two or three days. *Capillary water*, on the other hand, forms extremely thin films between the smallest particles or is taken into the colloidal fraction. Swelling of the soil colloids may take place so rapidly that all but the largest open spaces are filled in considerably less than an hour of rain. Beyond this point, erosion is likely to ensue. Mud is soil whose colloidal solids have become greatly dispersed with imbibed or capillary water. Capillary water is so firmly held to the soil particles by powerful adhesive forces that it moves through the soil extremely slowly. Therefore, contrary to opinions frequently held, it moves hardly at all toward an absorbing root. For this reason a root surface without hairs can receive water from a zone of soil only perhaps 15 mm. thick. Any water beyond this distance is practically out of reach. However, with root hairs of normal numbers and length, water becomes available from about four times as much soil.

For those species whose roots form large numbers of branches, both water and nutrients are correspondingly more available. The growth in length of roots and their branches, each with its migrating zone of hairs following close behind the apex, continually brings the absorbing portions into contact with new sources of capillary water. The remarkable amount of such migration through the soil can be recognized from the following results. A squash vine growing in a greenhouse was found to add an aggregate length of about 1000 feet of root per day, taking into account all branches and branchlets. In another study it was found that a single corn plant occupied, with its root branches, a cylinder of soil seven feet in diameter and six feet deep.

Farmers have known for a long time that the grain sorghums will produce a successful crop in climatic conditions or in years of drought that make the growth of corn impossible. An important part of the explanation of this difference seems to lie in the discovery that the sorghum plant produces twice as many root branches as a corn plant when growing under similar conditions. Thus the sorghum rootlets accomplish a more nearly complete penetration of every tiny segment of the soil, and absorb almost all the available water.

Soil Microörganisms. So complicated and so rapidly changing is the soil of a forest floor or of a fertile garden that it is all but impossible to visualize the numberless activities carried on by living organisms and by purely chemical reactions on any warm summer day. Besides the countless growing root tips there are hundreds of other kinds of living things. There are bacteria of many kinds living in the soil colloids, insects large and small, numerous species of earthworms, molds and a vast number of other plants and animals, all living together, each bringing about its own peculiar sets of activities.

All of these organisms respire and in so doing give off considerable amounts of carbon dioxide. This compound unites with water, forming carbonic acid, which, in turn, reacts with various minerals, forming more soluble substances. That is to say, the products of respiration help indirectly to make certain soil minerals available to plants.

Of the numerous kinds of bacteria, some secrete enzymes that digest the cellulose and other cell wall materials of the humus. This digestive action often requires several steps carried on by as many bacterial forms, but the final product is usually a sugar. These sugars, in turn, furnish the energy used in the metabolism not only of the bacteria concerned but also of many other microscopic organisms.

Other bacteria in the soil break down various proteins or their derivatives. At the end of this series, nitrates are formed. These may be absorbed by roots and used as a source of nitrogen in the metabolism of green plants.

All these activities which gradually destroy the humus are very complicated, because of the interaction of many kinds of microscopic organisms, each bringing about its single characteristic change in the soil. The products of any one step are then attacked by the enzymes produced by the next microbe of the series. So far as these bacteria are concerned this activity is one of digestion, but the total action is commonly considered as a unit and called *decay*.

Among the bacteria that live in the soil are certain ones that do not play a part in decay but, on the contrary, absorb the nitrogen of the atmosphere, and build it into their own protoplasm. This

process is called *nitrogen fixation*. Excretions given off by these bacteria while they are alive, and disintegration products of their bodies that are liberated when they die, become changed into nitrates, in this way adding fertility to the soil. These forms use as a source of energy (p. 57) the sugars produced by some of the organisms of decay.

Besides the soil-building processes carried on by microörganisms, important changes are brought about by some of the larger inhabitants of the soil. Among these, earthworms in humid climates and ants in arid places are of peculiar interest, especially because of the tunnels and burrows they construct. These multitudinous passageways act as channels through which gases can move freely into the upper layers of the ground and through which rain water descends. All animals, large and small, that make holes in the ground act as nature's plowmen.

The various examples given above are only a few representative samples of the multitude of interacting processes involving gases from the air, that take place in the soil.

Summary. Roots are, characteristically, the organs of anchorage and absorption of plants. Young root tips have cell walls that are readily permeable to water and dissolved minerals, and many of the epidermal cells of land plants extend out into the soil as root hairs. In this way the absorbing surface is greatly increased. These root hairs, delicate as they are, also afford a considerable amount of anchorage for the plant because they become firmly wedged between soil particles and the walls may even become gluelike. The thousands of root tips with their millions of root hairs are often so strong in the aggregate that when firmly anchored they do not permit the plant to become uprooted. Instead, the stem often breaks.

Absorption is, basically, osmosis, which is differential diffusion through a semipermeable membrane. That is to say, solutions, or their parts, enter or leave the root, each traveling from its own higher to its lower concentration, except when it is stopped by a membrane through which it cannot pass.

The soil is a reservoir of mineral nutrients. A rich soil is one in which all the necessary minerals occur in ample amounts and in such forms that they are readily available to plants. A poor soil may be deficient in only one or in several nutrients, or it may have some of them in an unavailable form or, in some instances, it may contain substances which are poisonous to plants.

Young roots are constructed of three parts: an outer single layer of cells—the epidermis, with its root hairs; a cortex, usually of pithlike cells, but with a more or less definite inner layer—the endodermis; and the stele, which occupies the entire center. The stele is, chiefly, a conductive structure. Commonly, xylem occupies the center of the stele, although sometimes the innermost cells do not differentiate entirely into conductive tubes. In such cases a pithlike tissue occupies the center, surrounded by the xylem proper. As seen in cross section, the primary xylem in the young root extends outward for a short distance in the form of rays, between which lie the masses of phloem. The outermost part of the stele is the pericycle which joins onto the endodermis, the innermost layer of the cortex. Root branches originate in the pericycle and a cambium may extend from it in such a way as to separate the xylem and phloem. If this cambium becomes active it produces secondary xylem and phloem. Xylem carries water from the roots to the stem and leaves, and phloem transports foods and minerals.

SUPPLEMENTARY READINGS

Cannon, "The Root Habits of Desert Plants."
"Conservation of Renewable Natural Resources," a symposium.
Curtis and Clark, "An Introduction to Plant Physiology."
"Hunger Signs in Crops," a symposium.
Kramer, "Plants and Soil Water Relations."

Chapter 8

THE STRUCTURE AND FUNCTIONS OF STEMS

Stems have two main functions: they support the leaves in the air and light where they can carry on photosynthesis and other metabolic processes in an efficient manner; and they act as channels through which water and solutes reach the leaves, and through which foods, hormones and other products travel to the roots and fruits.

Stems vary greatly in form, size, and structure. Those of trees, when sufficiently large and mature, are our sources of lumber.

The general outline of this chapter follows:

- Types of Stems
- The Leafy Shoot
  - Organization
  - Functions
- Cellular Structure of Young Dicotyledon Stems
  - The Stele
  - The Cortex
  - The Epidermis
- The Growing Tip of a Stem
- Older Dicotyledon Stems
  - Growth in Thickness
  - Growth Rings
  - Development of Bark
  - The Structure of Wood
- The Scattered Stele of Monocotyledons

Leaves do not grow directly attached to roots. And yet the necessary functions of synthesis and absorption take place at these two extremities of common plants. If they are to live, roots in the ground must have food produced in the leaves. Likewise leaves must be supplied with water, have access to carbon dioxide, and be exposed to the light if they are to manufacture carbohydrates; and the various parts of the plant must receive suitable minerals to be used in the building of protoplasm if growth and health are to be maintained.

The stem occupies a position between roots and leaves and may be regarded primarily as the framework which holds the leaves in a suitable position to carry on photosynthesis and the channel through which water, dissolved minerals, and foods travel between the leaves and roots.

The longest known stem of a seed plant is the trunk of a redwood tree growing near Dyerville, California. It stands 364 feet tall. On the other hand, stems of some rosette plants such as dandelion and plantain measure only a small fraction of an inch.

Types of Stems. Stems vary remarkably not only in length and size but in form. Some plants grow upright, some sprawl over the ground or on other supports, others take the form of vines and still others extend horizontally underground.

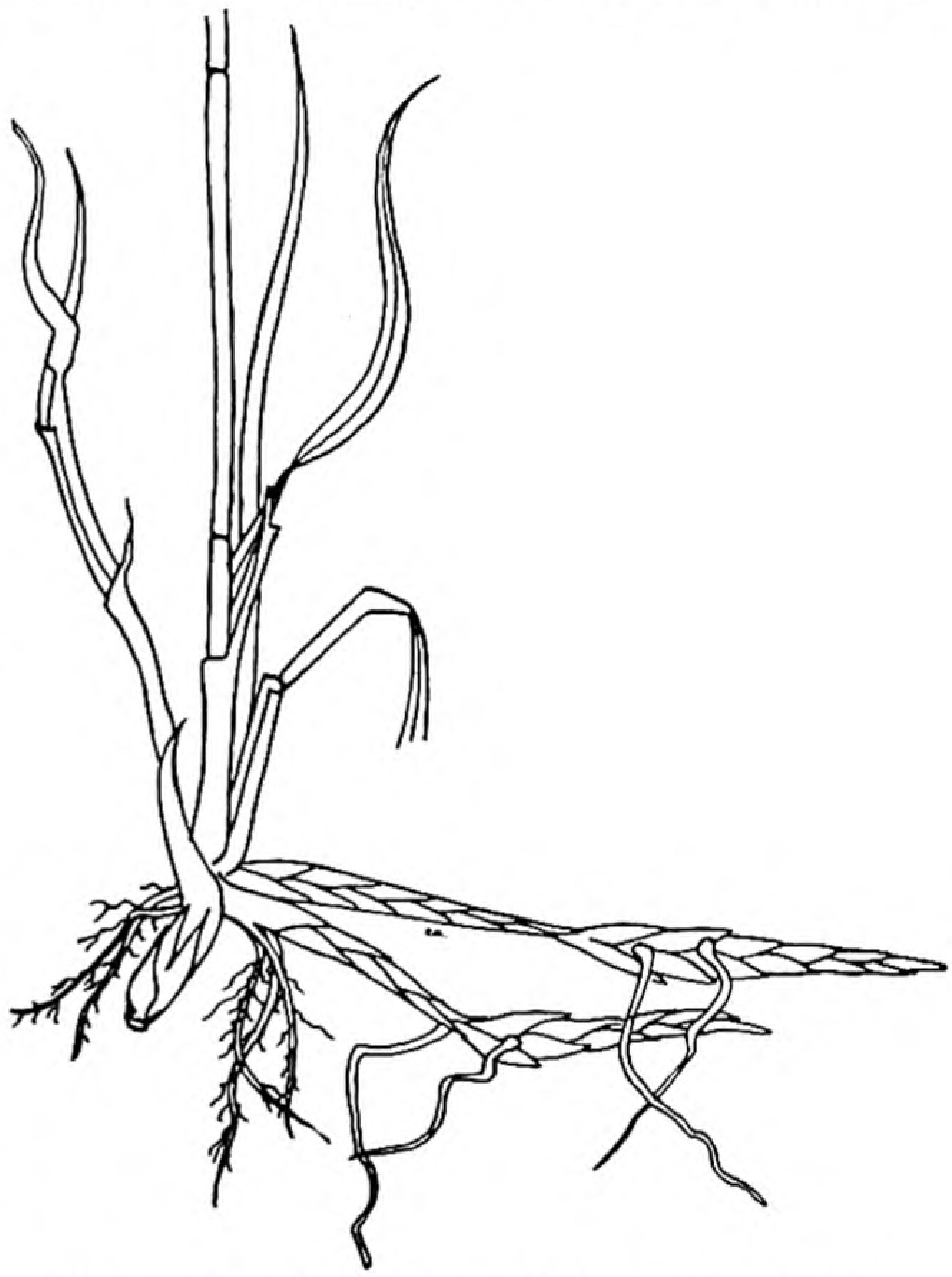
Some plants develop little wood. Recall as examples the various garden vegetables and farm crops, the weeds of cultivated fields and unkept city lots, the twining morning-glory, the prostrate melon and pumpkin vines, and the grasses and wildflowers of meadows and prairies. These are commonly referred to as *herbaceous plants* or simply as *herbs*. In contrast, other plants produce a great deal of wood. Woody plants take the forms of *trees*, *shrubs*, and *lianas*.

A *tree* is a relatively large woody plant, normally having a single upright stem, commonly called the *trunk*. Native forest trees of fir, pine, maple, beech, ash, walnut, oak, hickory, magnolia, and scores of others are common both as planted specimens and in groves and woodlands throughout the parts of this country that were forest-covered in the earlier days of this nation. Today, there are very few places where trees are entirely absent. In the great expanses of the grasslands hundreds of miles wide east of the Rockies, the early settlers of a century ago found hardly a shrub. But now, windbreaks of growing trees, especially of cottonwoods, shelter many of the homes on these same far flung plains.

Shrubs are much like trees, but are smaller, more profusely branched and often have several main small stems. Such well-known plants as roses, lilacs, blackberries, hazelnuts, sumacs, the smaller willows, and many of the foundation plantings about buildings are shrubs. This form of woody plant often makes up the chief undergrowth in forests, along stream courses, and even extends far beyond the forests into the grasslands and deserts.

Lianas are woody vines. Virginia creeper, grape, poison ivy, and clematis are well known examples. Such vines frequently grow as tall as the trees in which they climb. Their leaves, therefore, are well supplied with light. This type of long, slender climbing plant is especially common on the flood plains along rivers and in the towering tropical rain-forests and jungles, wherever they occur around the globe.

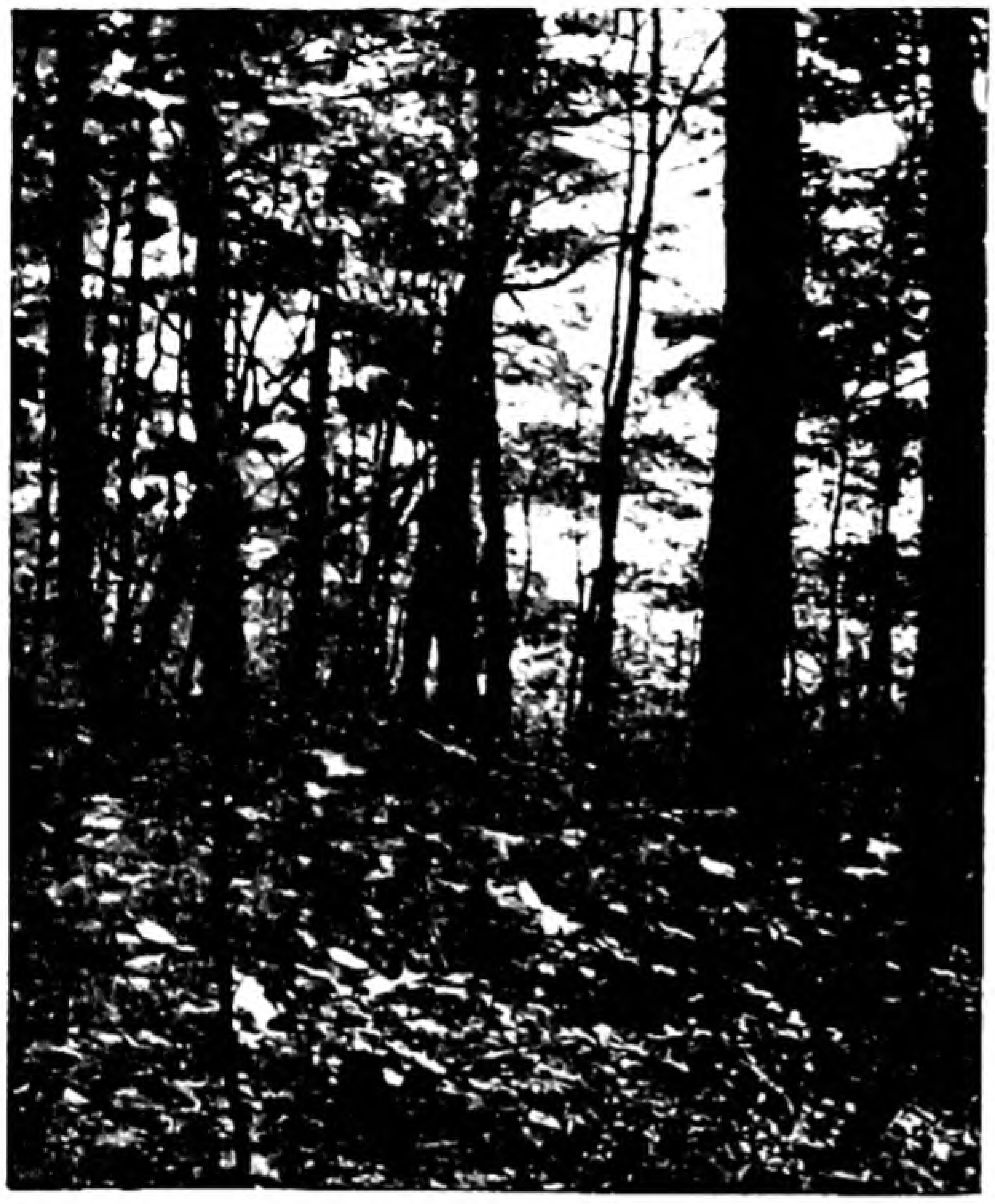
Not all stems grow in air. Instead, many plants have underground stems or *rhizomes*. The sod-forming grasses are good examples. Sod is a combination of branching rhizomes and numerous



Rhizomes, aerial stems, and adventitious roots of a grass.

adventitious fibrous roots growing from them. In addition to the grasses, many ferns, mints, and other common plants have underground stems. In many species upright branches arise from the rhizomes and grow above the ground, forming *aerial stems*.

Whatever the type of stem, whether it is woody or herbaceous, whether it grows in air or underground, or whether it is large or small, two characteristics set it off from roots. It always has nodes and either rudimentary or well developed leaves, or it has characteristic internal structures which will be discussed somewhat later in this chapter. Usually the nodes are not visible in the older stems of mature trees, shrubs, or lianas but are always evident on the younger twigs.



Sugar maple trees growing in a forest and in an open field. Note the differences in height of trunk and in growth of branches. Photograph at left in Allegany State Park. (Courtesy, New York State Museum.)

Plants with only relatively short aerial stems have root tips and leaves correspondingly near to one another. This arrangement is probably somewhat favorable as compared with that of a tall tree, because water and foods have only short distances through which to travel. On the other hand, the leaves of the short-stemmed forms are in danger of being shut off from the light by taller plants. Therefore, here as in many other situations met by living things, advantages and disadvantages tend to balance one another.

To some degree these several types of stems may vary according to the environment in which the plants happen to be growing. As an example, a sugar maple standing in an open field usually takes the form of a beautiful, symmetrical, round-topped tree of moderate height. If that same tree had matured in a forest, it would have grown much taller and would have remained more slender. Such variations as these are clearly responses to environment. But the limits of the degrees and types of responses any organism can give are set by hereditary factors. To illustrate, a violet or a fern growing in the open field will assume a somewhat different form from that which it would take if it were under the dense shade of a forest, but under no conditions is such a plant capable of taking on the shape or size of a tree. Likewise, a young tree growing in a bed of violets still remains a tree. The maple received from its ancestors the combination of genes which makes it a maple. Likewise, a violet or a fern is what it is because of the hereditary determiners that came from its parents.

The Leafy Shoot. An examination of a considerable number of leafy twigs shows that they differ from each other, not only in leaf shapes but also in the positions the leaves occupy on the twigs. The point on the stem where a leaf is attached is called a *node* and the parts between the nodes are *internodes*. Hence the nodes with their leaves are separated from each other by the elongation of the internodes between them. If the internodes extend greatly in length, the nodes are far apart, but if the internodes remain short, nodes and leaves are correspondingly nearer together. Nodes and internodes are very clearly seen as

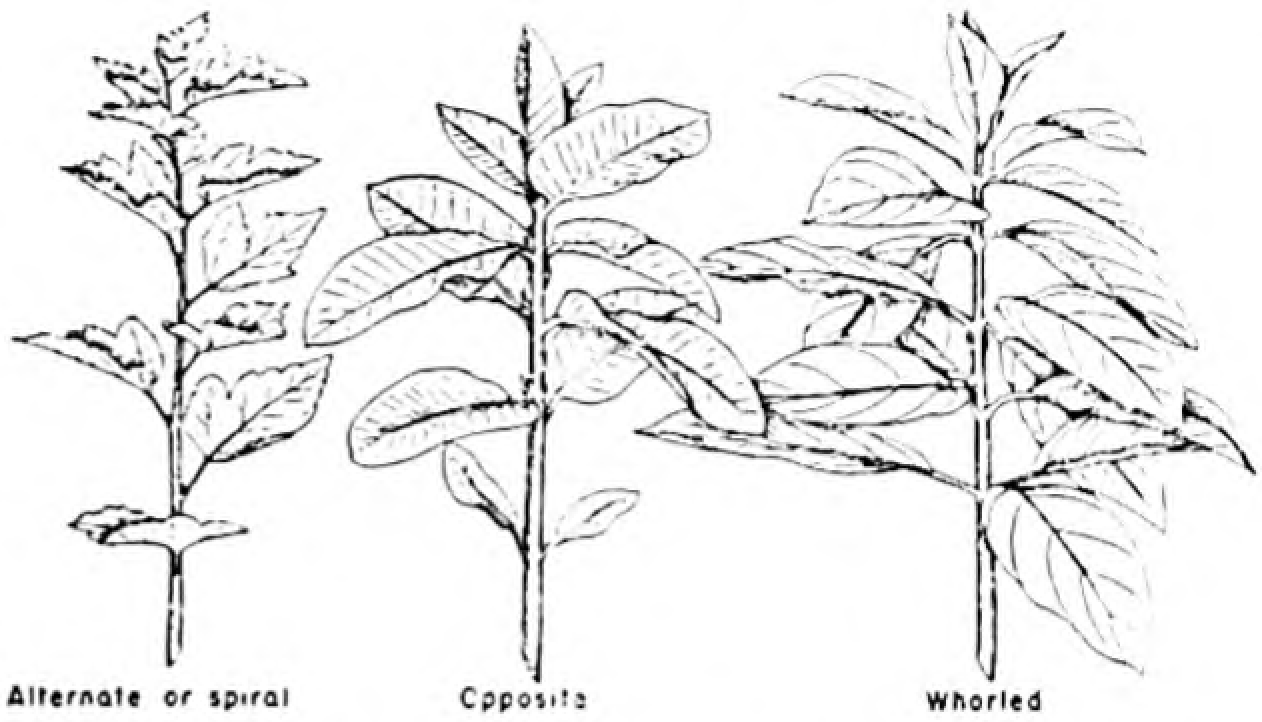
distinct structures in plants such as corn, bamboo, and many of the other grasses and in the smartweeds. In numerous other plants, however, these two parts can be recognized only as regions of the stem.

Usually at least one branch, or a bud, which is an undeveloped branch, is to be found at each node in the angle just above the point of attachment of the leaf to the stem. This angle is known as the *axil* (*axilla*, armpit) of the leaf, and the branch or bud is said to be axillary. Because such buds are attached to the side of the stem they are also sometimes referred to as *lateral buds* (*latus*, side). This arrangement of parts—a leaf attached to a stem, with a bud or a branch in the axil—constitutes a sort of general pattern according to which the shoots of all kinds of flowering plants seem to be built. In other words, angiosperms, with very slight exceptions, have the proper hereditary equipment, that is, gene complex, to cause them always to grow in this form, irrespective of environment.

In a few trees, such as the sycamore, there seems superficially to be no axillary structure but, on

Bamboo, showing jointlike nodes with long internodes between.

removing the leaf, it can be seen that the base of the petiole completely covers a bud. In certain herbaceous plants the axillary bud may be so small that it cannot be seen, but microscopic examination will



Common types of leaf arrangement. (*Left*) Ninebark. (*Center*) Milkweed. (*Right*) Hydrangea.

usually reveal its presence, or an injury to the part of the stem above the attachment of the leaf will often stimulate the growth of a branch. In some plants there may be more than one bud on the stem above the leaf. In this case the additional ones are called *accessory buds*. These may be placed in a row above the axillary bud, as in hickory or walnut, or clustered at its sides, as in maple or *Forsythia*. These extra buds are often larger than the axillary one and frequently develop so vigorously that the axillary bud is completely suppressed.

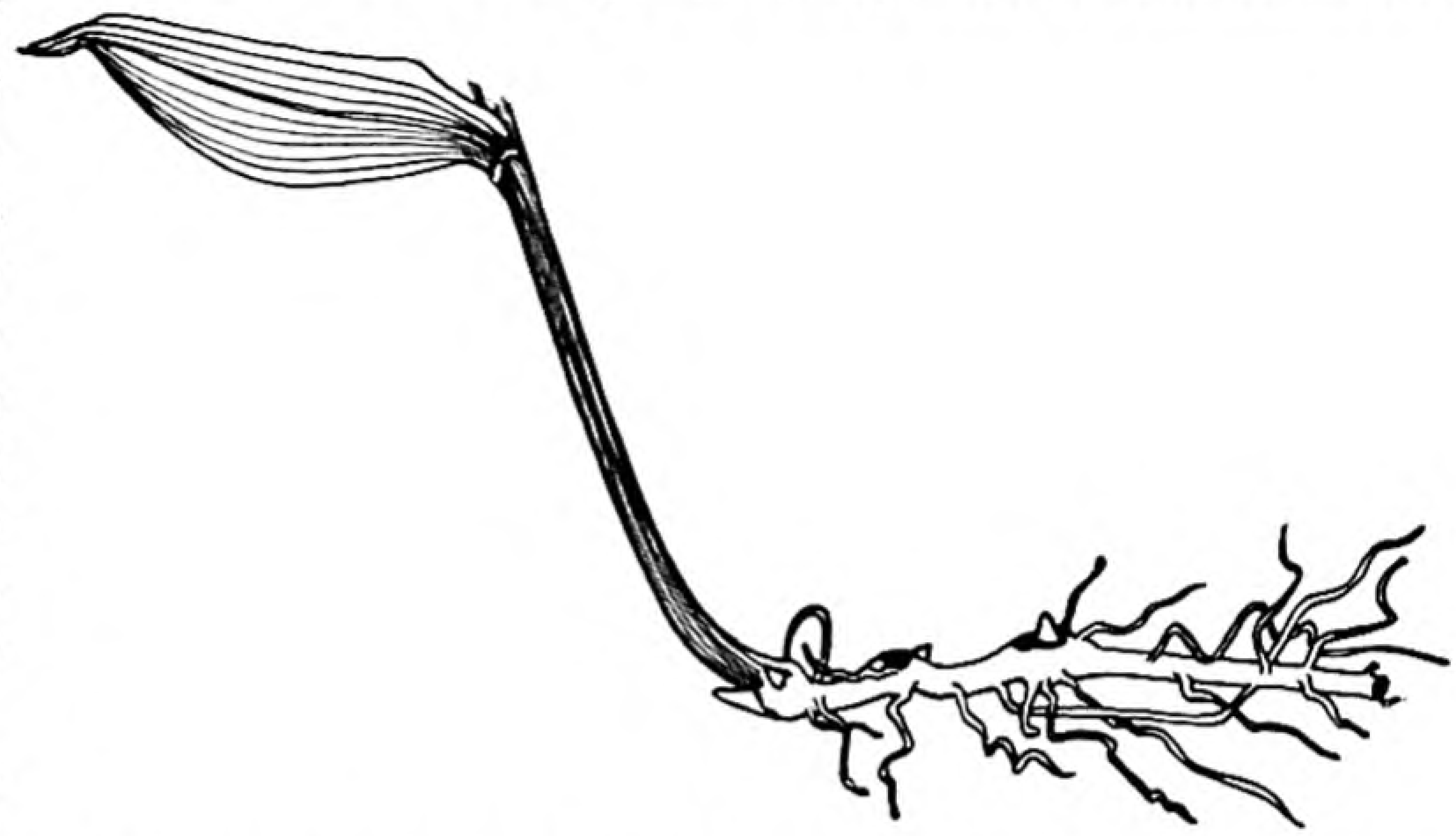
Leaf Arrangement. In some plants the leaves are attached singly, one at a node, on the stem. This type is called *alternate* or *spiral arrangement*. If a line is drawn from a leaf around the stem to the one next higher and then to the next, and so on throughout the length of the stem, the line follows a spiral course. In other plants the leaves are in pairs at each node. This is called *opposite arrangement*. In still others they are in *whorls* of three or more. Many plants which ordinarily have opposite leaves occasionally have a vigorous shoot on which the leaves occur in whorls.

If the internodes of a twig lengthen only slightly, the leaves are so crowded that it may be difficult to determine arrangement. In such cases it is only necessary to examine other parts of the same plant in which the internodes have grown sufficiently to separate the nodes. In winter, when the leaves

have fallen, the leaf arrangement can be determined by noting the location of the buds and leaf scars.

Buds. DORMANT BUDS. Throughout the world, with the exception of certain limited parts of the tropics, there are seasons of cold or of great dryness. Under either of these conditions plants must become inactive because metabolism in all its phases is retarded or almost entirely stopped by low temperatures or by reduced supplies of water. With the beginning of the cold of autumn and winter or of the drought of the dry seasons, various plants react in different ways. Some die, but the majority develop inactive or dormant buds.

These buds are most easily seen at the nodes on the twigs of trees and shrubs, but they are present on the underground stems of such low growing plants as the grasses, violets, ferns, and Solomon's seal. Those that form underground, however, are often little different from growing buds that cease, temporarily, to be active. On the other hand, the majority of those on woody perennials are of a more complicated character.



Rhizome of Solomon's seal, showing slightly dormant underground buds in winter.

Twig of apple tree in winter condition, showing a short branch that has been elongating very little for many years, making leaf arrangement difficult to determine. On the lower part the buds and leaf scars are clearly alternate.

In order to understand winter buds a collection of dormant twigs of as many kinds of trees and shrubs as possible should be made. A great variation will be seen in the length of the season's growth in different species and even on branches of the same individual tree or shrub.

If all the leaves have fallen each lateral or axillary bud has below it a *leaf scar* which was left by the breaking away of the petiole of the leaf of the previous growing season.

A winter bud consists of three parts: a series of protective scales on the outside, a number of undeveloped leaves surrounded by them, and at the center, an apical meristem. The bud scales are considered to be specialized leaves because their early development from the apical meristem takes place in the same way as that of leaves; because under experimental conditions the rudiments of scales can sometimes be caused to become foliage leaves; and because in some trees, such as the box elder, every gradation between scale and leaf regularly occurs. The apical meristem is the essential structure, while the outer scales protect the delicate inner parts from mechanical injury and from drying. Students frequently suppose that the scales protect against cold, but this is incorrect because the inside of a bud is known to become practically as cold as the air outside.

In some plants the bud scales are hard and dry; in

others, soft and fleshy; and in some species their protective value is increased by a covering of hairs or by a water-proof, resinous secretion.

Even more important to the survival of dormant buds is the fact that the protoplasm of their cells

Winter buds. (A) Cottonwood twig with terminal bud and several lateral buds. The lowest of the lateral buds has grown into a short branch. Two terminal bud scars show the positions occupied by the terminal bud, one and two years before, respectively. (B) Section through winter bud showing apical meristem surrounded by young leaves, which are, in turn, covered by three layers of bud scales.

loses a part of its water and accumulates sugars and other soluble substances. Together, these changes greatly increase the concentration of dissolved materials in the protoplasm. As we have seen, the more concentrated the solution, the lower will be its freezing temperature. Therefore, these dormant buds are actually able to withstand relatively low temperatures without the formation of ice crystals within their protoplasm.

In addition, certain changes that are not fully understood take place in the cell colloids, making the protoplasm better able to resist the harmful effects of both drying and freezing.

When a terminal winter bud begins to grow in the spring, its short internodes elongate, gradually increasing the distance between the nodes; the embryonic leaves enlarge, unfold, and take on the mature organization; and the scales that have covered the bud fall away leaving the *terminal bud scars*. These marks may remain visible for several years until obscured by the formation of the outer bark. Whenever they can be seen clearly on a twig it is possible to learn its age.

ACTIVE OR GROWING BUDS. In autumn and winter it is easy to reach the conclusion that almost all buds are dormant, but this is far from true. During the growing season even the buds which are to become dormant during the ensuing winter are active, growing structures.

In addition, many kinds of plants such as garden vegetables, field crops, house plants, and plants of the moist tropics seldom have the ability to form dormant buds even where subjected to cold or drought. Instead, they die under these conditions.

An actively growing leaf bud is constructed of an apical meristem surrounded by a group of young developing leaves. There is very little difference in appearance between the growing bud that is able to become dormant and produce bud scales and one that does not have this power. The difference lies in the hereditary capacities of the two plants.

FUNCTIONS OF BUDS. The terminal bud is primarily an apical meristem whose cells are capable of dividing actively. This meristem moves forward as it grows, extending the length of the stem, leaving behind it a succession of nodes with their leaves and lateral buds or branches, and with internodes between. Lateral buds have apical meristems with the same capacities as those of the terminal ones. Depending on circumstances, they may remain inactive indefinitely, or may grow, producing branches.

Aside from the leaf buds described thus far, there are also *flower buds* and *mixed buds*. Ordinarily, when an apical meristem gives rise to a flower bud, the meristematic tissue is all changed into floral structures. In the case of mixed buds both flower and leaf primordia are organized, permitting flowers and leafy shoots to develop together.

In addition, another function of growing buds is the manufacture of growth substances that greatly

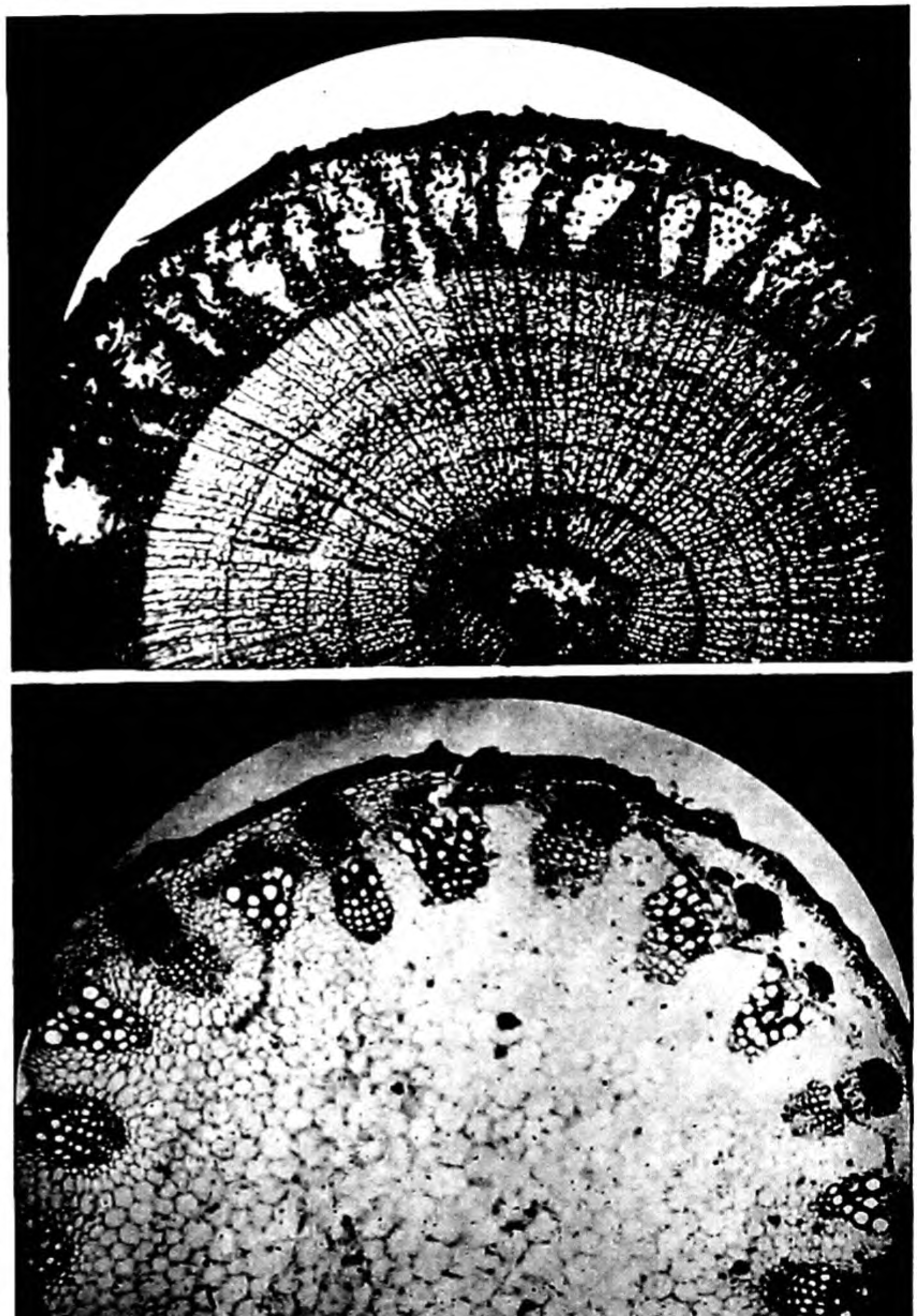
influence the form and many activities of the plant.

Stem Functions. The leafy twig is made up not only of leaves and buds, but also of *stem* which supports them all and acts as a channel through which water, food and growth substances travel.

The support of leaves and the transfer of materials between leaves and roots are possible because of certain specialized groups of cells in stems. These cells, in turn, are unable to function properly without the presence of others. In other words, the stem is a highly organized part of the plant, and it should be understood that the young root, stem, and leaf are all constructed of about the same set of tissues which are continuous throughout the plant.

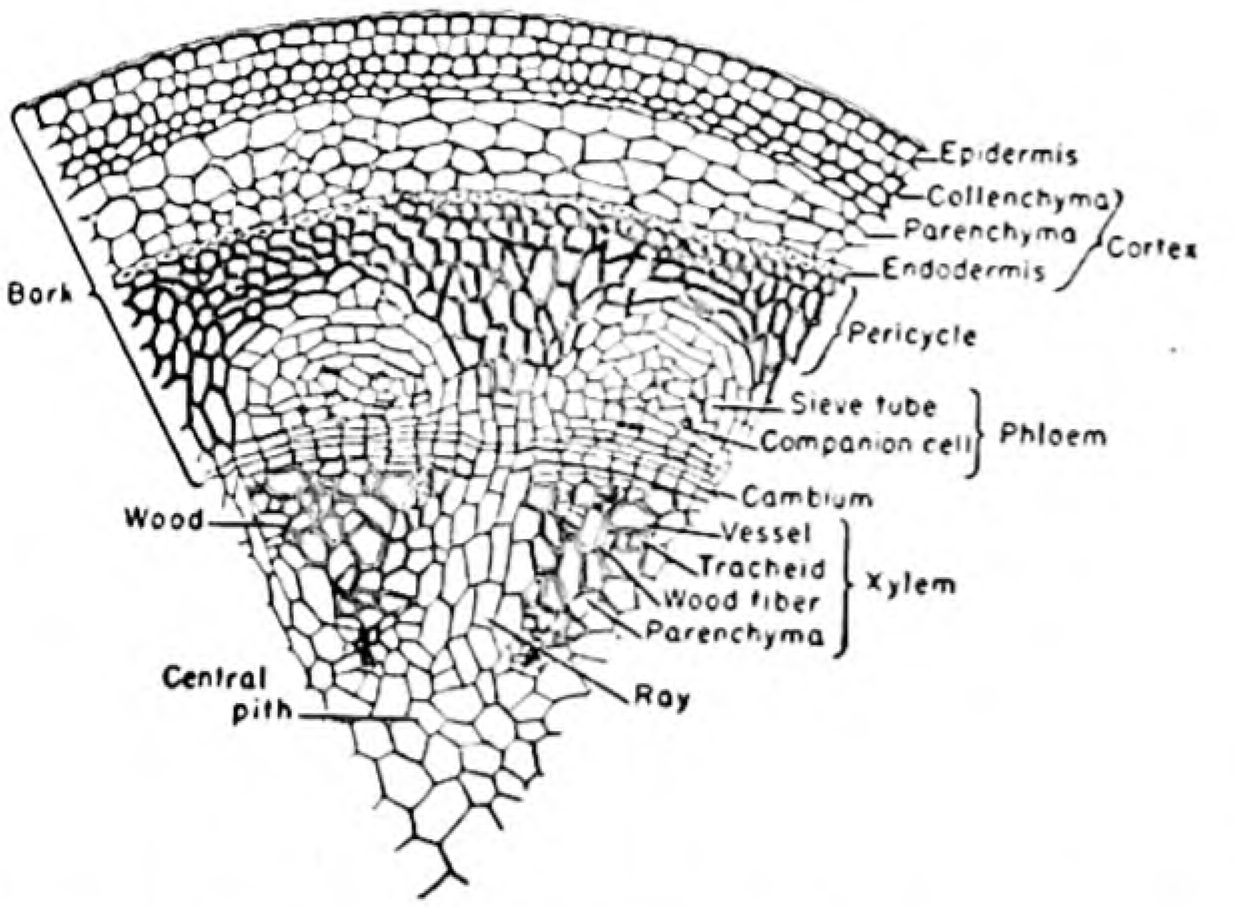
Notwithstanding the fact that almost all stems carry on much the same kinds of activities, there are considerable differences in the arrangement of tissues in different types. For this reason, in order to understand the functioning of the stems of common plants, it is necessary to become thoroughly acquainted with the typical anatomy of both dicotyledons and monocotyledons.

Cellular Structure of Young Dicotyledon Stems. If transverse sections of the stem of a wide variety of dicotyledons such as geranium, sunflower, and young woody twigs of maples, elms, linden trees, and willows, are compared by means of the microscope, they are found to be similar in many respects. Sizes of the various parts vary with species and age, but types of structures and relative positions are the same in all. Occupying the center in each is the central pith around which is the wood, and beyond the wood is the bark. The terms, wood and bark, are used here only for convenience because they are commonly comprehended, but with further study it soon becomes evident that



Dicotyledon stems. (*Top*) Linden. Notice the small central pith surrounded by five growth rings in the wood (xylem). A layer of cambium, almost too thin to be seen in the photograph, surrounds the wood. All the tissues outside the cambium are called collectively, the bark. (*Bottom*) Sunflower. The central pith constitutes all but a small outer zone of this stem; the wood (xylem) takes the form of bundles of cells just outside the pith; on the right side, the irregular dark line of cambium marks the inner boundary of the bark.

these names do not agree entirely with the structures and functions of the parts present. The illustration below gives the two sets of names in such a way that they can be compared.



Cross section of young stem with common and anatomical names of parts.

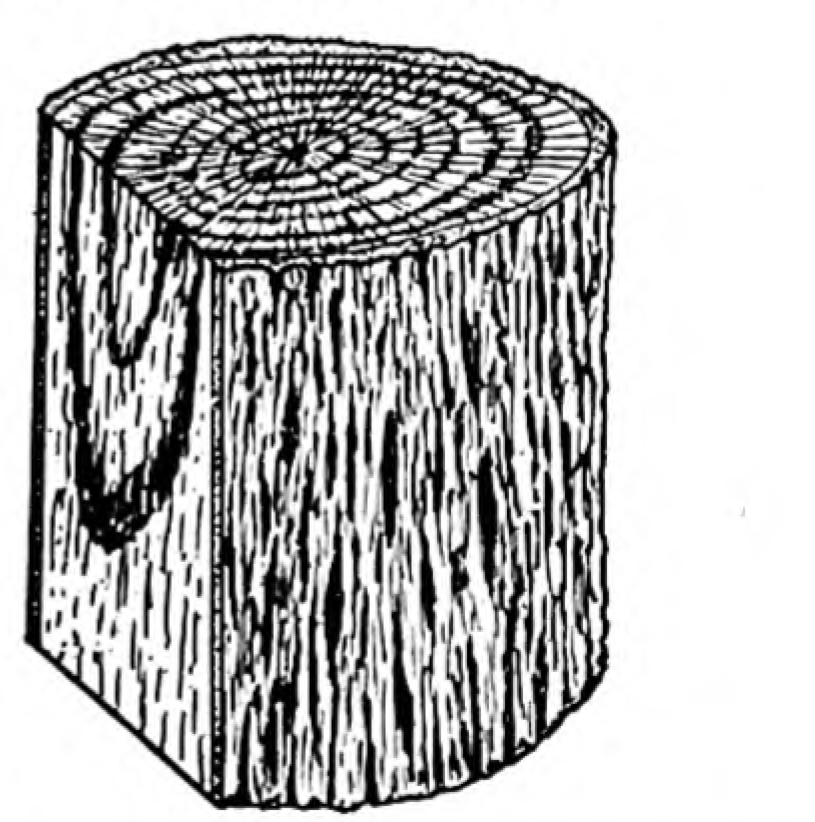
What is commonly called the bark of a young stem is a combination of the epidermis, the cortex, the pericycle, and the phloem. In other words the term refers to all the structures from the cambium outward. Inside the cambium lies the xylem. This is a complicated group of tissues usually thought of as a single unit and called wood. The central pith occupies the center and is surrounded by xylem.

From the standpoint of the organization of the plant as contrasted with the superficial appearance, there are three functional regions. These are the *epidermis*, a single protective layer of cells covering the underlying tissues; the *cortex*, which occupies the space inside the epidermis extending to and including the *endodermis;* and the *stele*, which includes all the tissues beginning with the *pericycle*, and continuing to the center. Both in stem and root, the endodermis is the inner layer of cortex and the pericycle is the outermost part of the stele. In some stems these can be clearly distinguished from one another; in others they are very indistinct. Both the stele and the cortex are more complicated and more varied in structure than the corresponding parts of the root with which they are continuous and into which they merge.

THE STELE. The stele is composed of pericycle, phloem, cambium, xylem, rays and central pith. As in the root, it is primarily a group of conductive tissues. In addition, certain of these cells commonly have thick walls that give mechanical strength to the stem.

CENTRAL PITH. This tissue is at the center of the stele and, therefore, of the stem. In some species such as parsnips and smartweeds, it breaks down in part soon after it is formed, leaving the stem hollow. Central pith appears to have little except occasional function as when reserve starch accumulates in its cells. It is certain that it plays no significant part in the primary values of the stem to the plant. Its thin-walled cells loosely fitted together can neither add rigidity to the stem nor act as an effective conductive tissue.

XYLEM. The terms xylem and wood are almost synonyms. Xylem, however, has a more exact meaning and is more commonly used in botanical work. A microscopic examination of cross sections of stems of common dicotyledons shows that this woody zone is made up of several kinds of cells. One of the most obvious of these is so arranged that lines or strips are formed extending outward away from the center of the stem. These lines or strips are called *xylem rays*. Some of them are continuous with the central pith and others may originate farther out in the wood.



Block of wood showing rays cut lengthwise and transversely.

If a stem is cut lengthwise and the rays are examined with a hand lens or with a microscope they are found to be platelike layers of cells with their edges directed upward and downward. In

other words, they are like thin blades thrust into the wood.

The functions carried on by the rays are usually considered to be the transfer of foods and water from cell to cell across the xylem with occasional temporary storage of starch. In addition, intercommunicating intercellular spaces permit the diffusion of such gases as oxygen and carbon dioxide throughout the woody tissues.

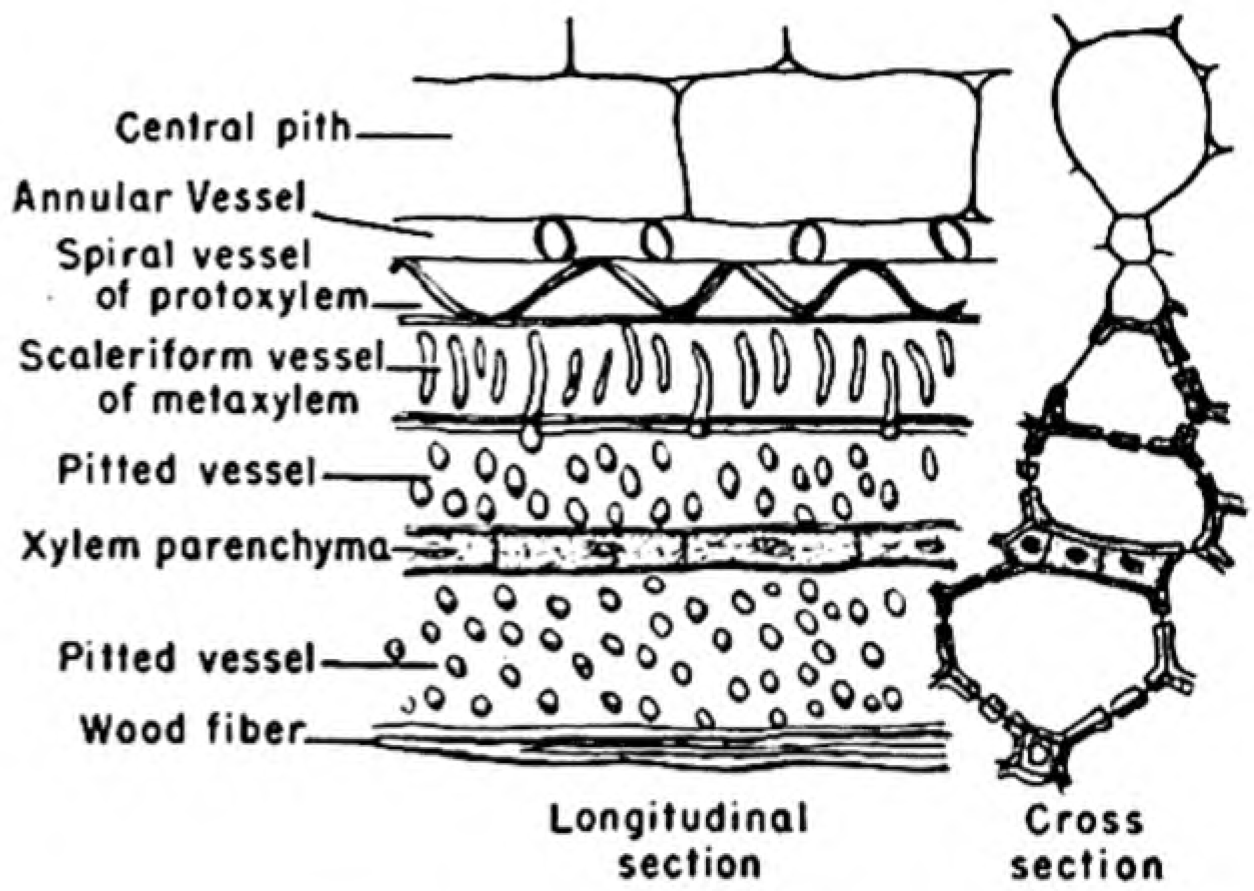
Aside from the rays the remainder of the xylem is constructed mostly of *vessels*, or *water tubes*, *tracheids*, and *wood fibers*. All of these extend lengthwise in the stem. Therefore, in cross section they are seen as the open ends of larger and smaller tubes. The largest are the vessels. Packed in between them are numerous smaller, thick-walled cells, the larger of which are tracheids. These grade gradually into the smallest forms, the wood fibers. Another type of cell that can be found frequently is called *xylem parenchyma*.

The parenchyma and most of the ray cells usually retain their active protoplasm throughout the life of the stem or, in the case of long lived perennials, for at least a considerable number of years. This type of behavior is in contrast with that of the vessels, tracheids, and wood fibers. In all of these the protoplasm remains well organized and active only until it has brought about the construction of their thick, woody walls. These walls are composed of a derivative of carbohydrates, called *lignin*. When these lignified structures have been completed, the protoplasm dies and disappears.

The mature fibers and tracheids originate as greatly lengthened individual cells. Each vessel, on the other hand, is formed from a series of cells of relatively large diameter placed end to end. The side walls of these cells become lignified and thickened and many of the end walls disappear, leaving long open tubes.

Wood fibers seem to have the single function of giving mechanical strength to the xylem. Their walls are so thick that they frequently almost close the space called the *lumen*, originally occupied by the protoplasm, thereby reducing conduction. On the other hand, the lumina of both tracheids and vessels are larger, forming small conductive tubes through which water moves freely. Since their walls are greatly thickened, these tubes, as well as the wood fibers, strengthen the stem.

The xylem cells that are first to differentiate, form at the outer surface of the central pith. They are



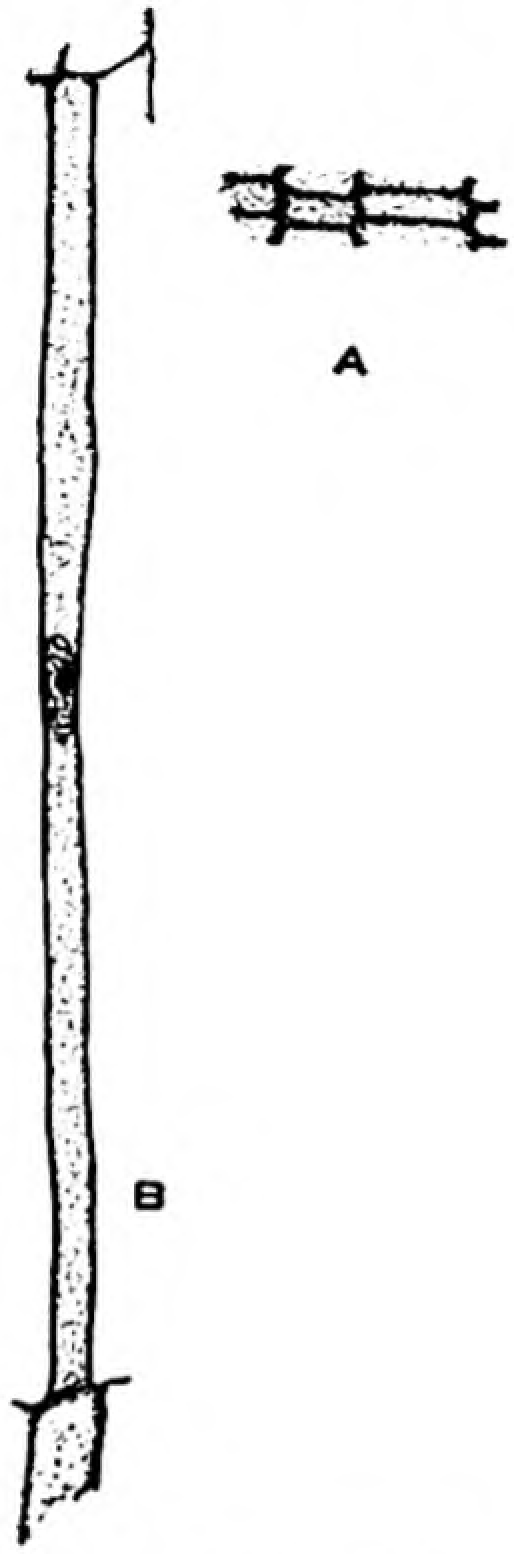
Xylem elements.

reinforced by a series of internal rings and spirals, making what are called *annular* (*annulus*, a ring) and *spiral vessels*. These vessels constitute the *protoxylem* (*protos*, first) because they are the first xylem elements that are formed in the young growing stem tip. Their walls are thin except at the places where the rings or spirals are attached, thus permitting the walls to lengthen with the growth of the stem in the region of elongation. When elongation has ceased, *metaxylem* (*meta*, after) is formed. The walls of these vessels and tracheids become thickened throughout, except in definite thin places which take two forms, long transverse slits as in the *scalariform* elements (*scala*, a ladder) and rounded or elliptical *pits* as in the pitted vessels. Protoxylem and metaxylem together constitute the *primary xylem* to be discussed later (p. 98).

CAMBIUM. Immediately outside the xylem is a layer of cells, the *cambium*. As in many roots, this forms the boundary between the xylem and the phloem, but cannot be seen as a definite structure without considerable magnification.

The only known function of cambium is the building of new tissues. In other words, it is a meristem. As seen in the cross section of a stem, cambium cells are usually more or less brick-

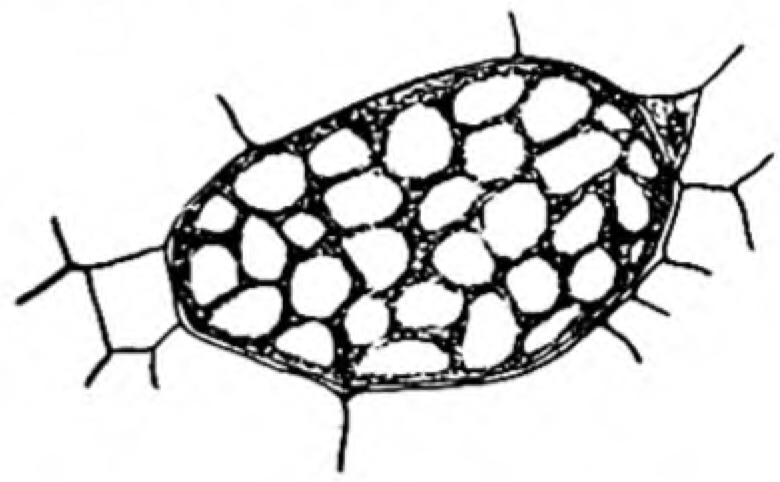
shaped, and their walls are extremely thin. If examined in longitudinal sections they are found to be relatively long and often spindle-shaped.

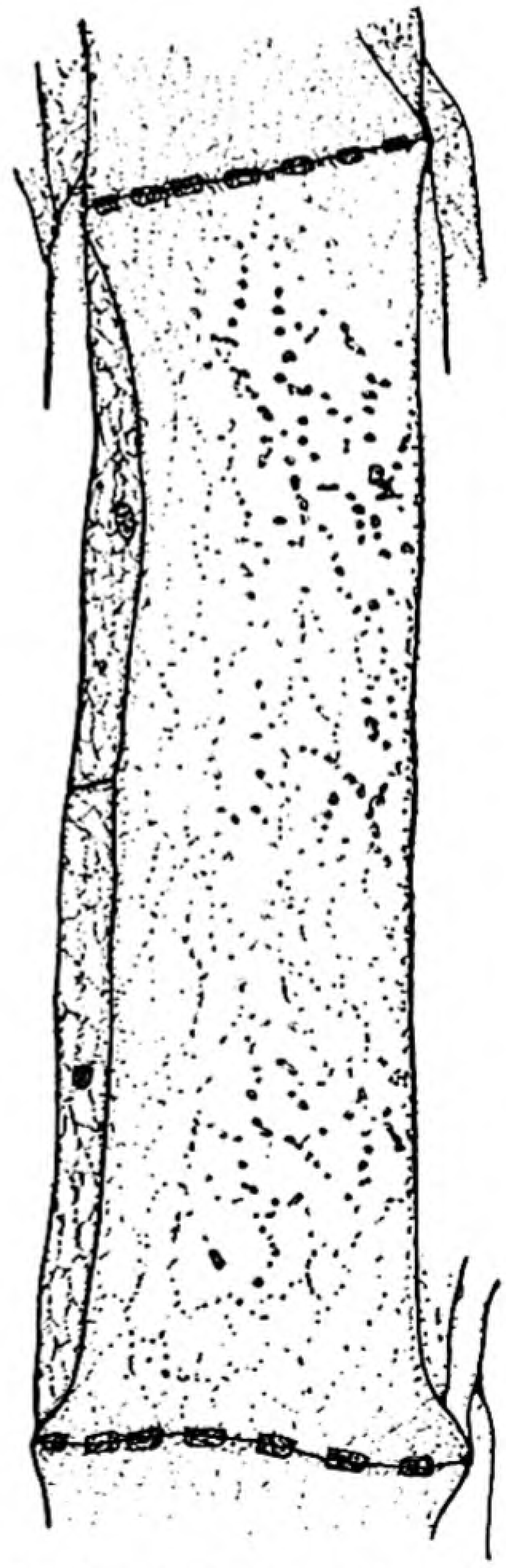


Cambium cells. (A) Cross section. (B) Longitudinal section.

PHLOEM. Phloem always extends parallel with the xylem throughout the length of root, stem, and leaf. Its primary function is the transfer of foods and growth substances from the leaves or other centers of synthesis to all other parts of the plant. The phloem of a dicotyledon stem is commonly made up of three kinds of cells. They are *sieve tubes*, *companion cells*, and *phloem parenchyma*. The thin-walled sieve tubes are formed of rows of *sieve cells* joined end to end. A sieve cell and its companion originates by a mitotic division of a mother cell. This mother cell is derived in like manner from cambium. The companion cell develops a large nucleus and at about the same time the nucleus of the sieve cell disintegrates. Cyclosis within the cytoplasm slows and then stops. In this condition the half-living sieve cell may remain from a few days to one or two growing seasons before it collapses.

The most conspicuous visible characteristic of a sieve cell is the *sieve plate*. This is a markedly pitted portion of a wall that separates two cells which fit together end to end. At the bottom of each pit there are large numbers of very fine perforations which permit protoplasmic connections between the adjoining cells. Although the significance is





Sieve cell. (*Top*) Cross section showing large sieve plate and small, triangular companion cell. (*Bottom*) Sieve cell and companion cells in longitudinal section.

not known, there are also protoplasmic connections with the companion cells. When a sieve tube is about to collapse, a considerable mass of material, called the *callus*, is deposited on the sieve plate.

The space around the sieve tubes and companion cells is filled with thin-walled *phloem parenchyma*, which is usually difficult to recognize in cross section. These parenchyma cells function in a variety of ways in different plants. Usually they act as starch-accumulation centers. Rather frequently they elongate and develop thick walls, becoming fibers that add greatly to the strength of the stem. Extreme examples of such fiber production are flax and hemp, in which phloem (sometimes called *bast*) fibers are of great commercial value. In perennials, phloem parenchyma sometimes organizes into a cork cambium which forms *periderm*. (See p. 141.)

Experimental evidence shows that the phloem is the most important channel through which foods and growth substances are transferred throughout the plant. How this is accomplished, however, and to what extent phloem shares this function with other tissues is at present a matter of much uncertainty.

PHLOEM RAYS. The *vascular rays* are made up of the xylem rays, already mentioned (p. 105) together with the *phloem rays* which are continuous with them, extending through the cambium.

PERICYCLE. In the stem, the pericycle is often difficult to distinguish. Sometimes it is composed of a few pithlike cells having much the appearance of phloem parenchyma. When it takes this form it practically merges with the phloem and cannot definitely be recognized. In some species the pericycle of the stem develops in the form of a complete band or of a series of groups of thick-walled strengthening fibers called *sclerenchyma*, just outside the phloem. In others, certain cells within the phloem take this form.

SIPHONOSTELES. Stems of almost all dicotyledonous plants and of gymnosperms have a central pith surrounded by xylem and phloem. This type of stem structure is known as a *siphonostele* because the wood or xylem is in the form of a tube or siphon. Siphonosteles are of two general types, *continuous* and *dissected*.

A great many plants have a stem structure in which the xylem, cambium, and phloem, interrupted only by very narrow rays, form an almost unbroken covering around the central pith as shown in the upper photograph on p. 104. This is called the *continuous siphonostele*. The stems of a large number of garden and house plants such as geraniums and begonias, and of trees and shrubs such as oak, elm, cottonwood, maple, apple, privet, and lilac, take this form.

Other common dicotyledons have a similar general structure but differ in that some or all of the interrupting rays are wide enough to separate the other conductive tissues into definite *vascular bundles* (the lower photograph on p. 104). A stem of this type is called a *dissected siphonostele*. Such plants as clover, pumpkin, potato, Dutchman's pipe (*Aristolochia*), and sycamore have this kind of stele. Very young stems usually have the dissected form even though they later develop the continuous type.

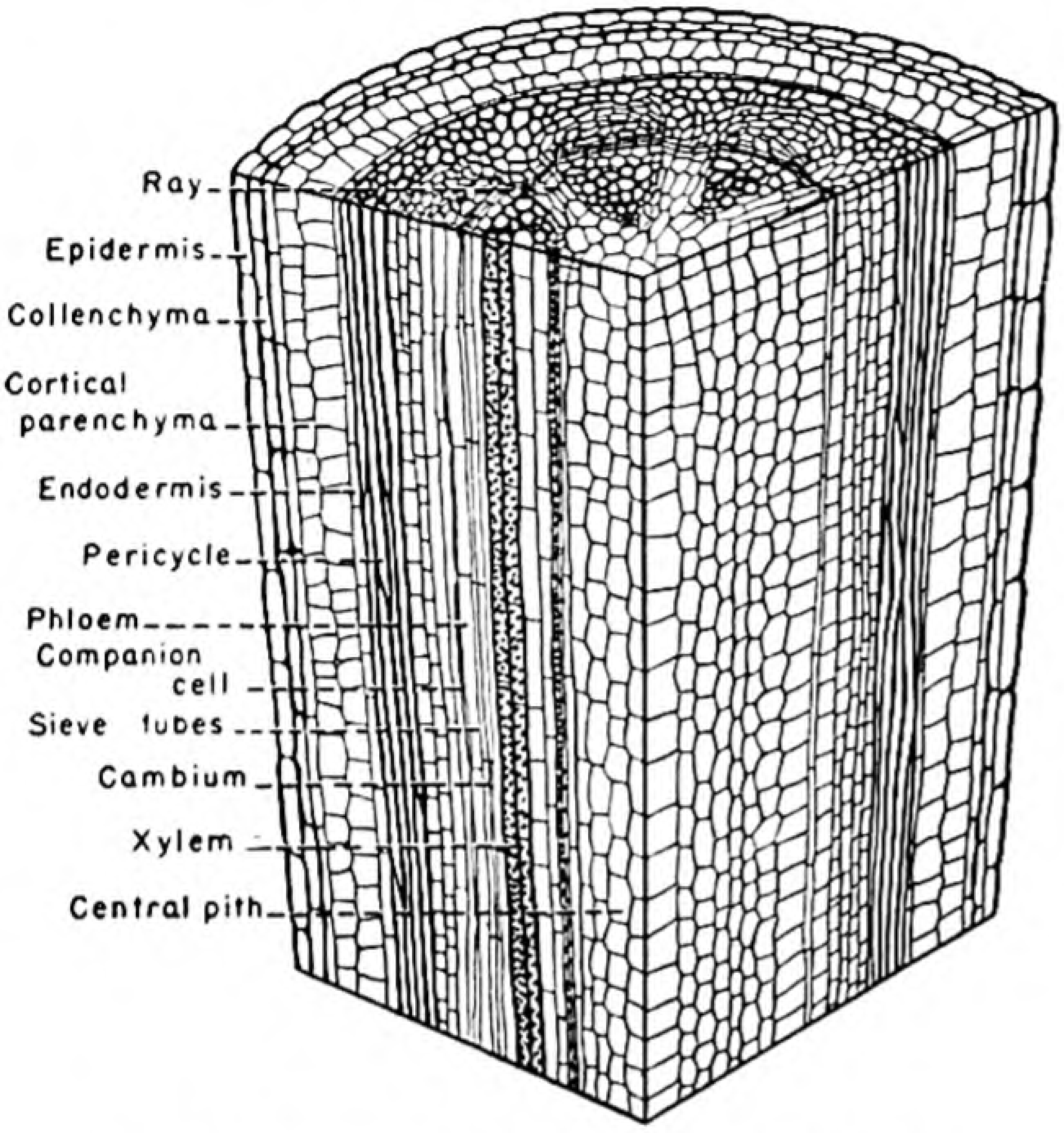
THE CORTEX. In the stem the cortex is often composed of several kinds of cells. Among the commonest are *endodermis*, *collenchyma*, and *parenchyma*.

ENDODERMIS. The endodermis is a cylindrical sheath of tissue one layer of cells in thickness. As in the root, it is commonly considered to be the innermost part of the cortex, and is attached directly to the pericycle. In some stems it is not visible at all, but in many it can be recognized as a definite layer by peculiarities in the size and shape of its cells, by the corky or lignified nature of their irregularly thickened walls, and by a generous supply of starch whose presence can be demonstrated by mounting thin sections in iodine.

COLLENCHYMA. Just beneath the epidermis, and particularly at the corners of angular stems, there occurs frequently a tough, fibrous tissue known as *collenchyma*. It can be recognized by the fact that the walls of its cells have conspicuous cellulose thickenings in the corners. This tissue frequently contains chloroplasts and probably carries on some photosynthesis as well as affording a certain amount of mechanical strength to young stems. Collenchyma combines strength with flexibility.

PARENCHYMA. There still remains a background of rounded, thin-walled, loosely arranged cells

which fill the spaces between the more specialized parts that have been discussed above. This is known as the pith, or *parenchyma*. Even this tissue sometimes shows a degree of differentiation, its cell walls being thickened to the point where it



Semidiagrammatic drawing of young stem.

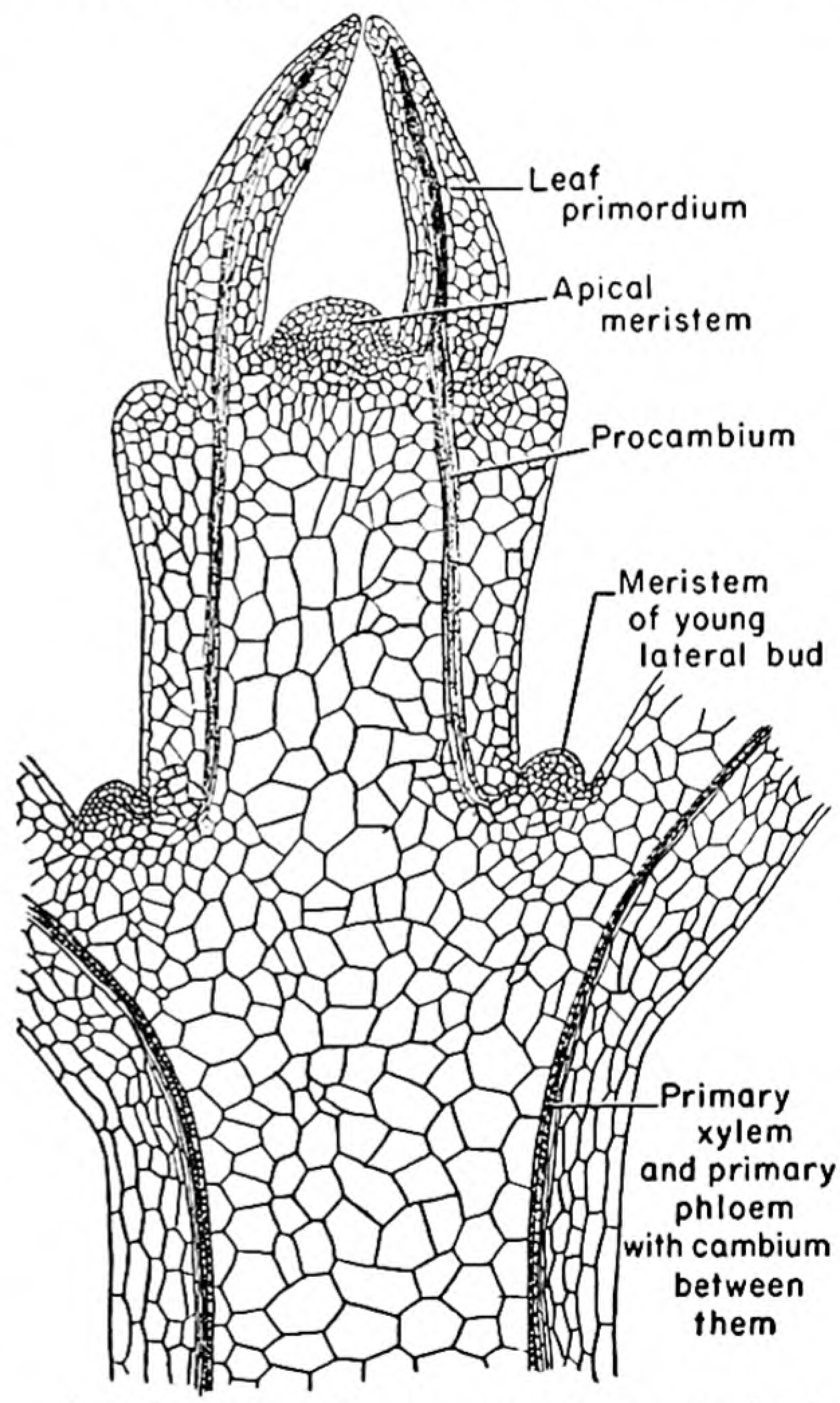
resembles some other tissues. On the other hand, it is usually so little specialized that it sometimes regains the characteristics of a meristem which grows and gives rise to new parts many months or even years after it first develops. The cortex, central pith, and rays are often made up of a tissue of this kind.

CHLORENCHYMA. All tissues which contain chloroplasts are sometimes known collectively as *chlorenchyma*. The green color of stems is usually due to chloroplasts in the cortical cells just beneath the epidermis, although in some plants chlorophyll may be found in the rays, occasionally even extending along them to the pith in the center of the stem.

THE EPIDERMIS. As in the leaf and young root, the outermost layer of cells of a young stem is the epidermis. There are usually fewer stomata per unit area in the surface of a stem than there are in that of the leaves. In most respects, however, the epidermis of a stem is much like that of the leaves and is continuous with it.

SUMMARY OF YOUNG DICOTYLEDON STEM. The illustration above ties together in proper order the numerous tissues that have been described in some detail in this section, showing their characteristics as seen in both longitudinal and transverse sections of the stem.

The Growing Tip of a Stem. Thus far these discussions have dealt with stem structure as if it were unchanging, but even casual observation



Apical region of stem as seen in longitudinal section.

shows that stems become both longer and larger in diameter with the passage of time. Growth in diameter depends largely on the action of cambium, while growth in length takes place primarily at the apex.

Beginning with the older parts of a vigorously growing shoot and approaching the tip, the leaves are found to be gradually smaller and younger until the youngest are so very small that they cannot be seen without some magnification. If our sight were keen enough, it would be possible to remove the youngest of these and find a growing tip or *apical meristem* much like that of a root, except that it is protected by developing leaves rather than by a root cap. This meristem with its developing leaves is an active bud.

The growing tip is understood better if longitudinal sections of it are examined with a microscope. It is made up of small thin-walled cells. These cells are composed of compact, rich protoplasm. As in the root tip they grow and divide rapidly.

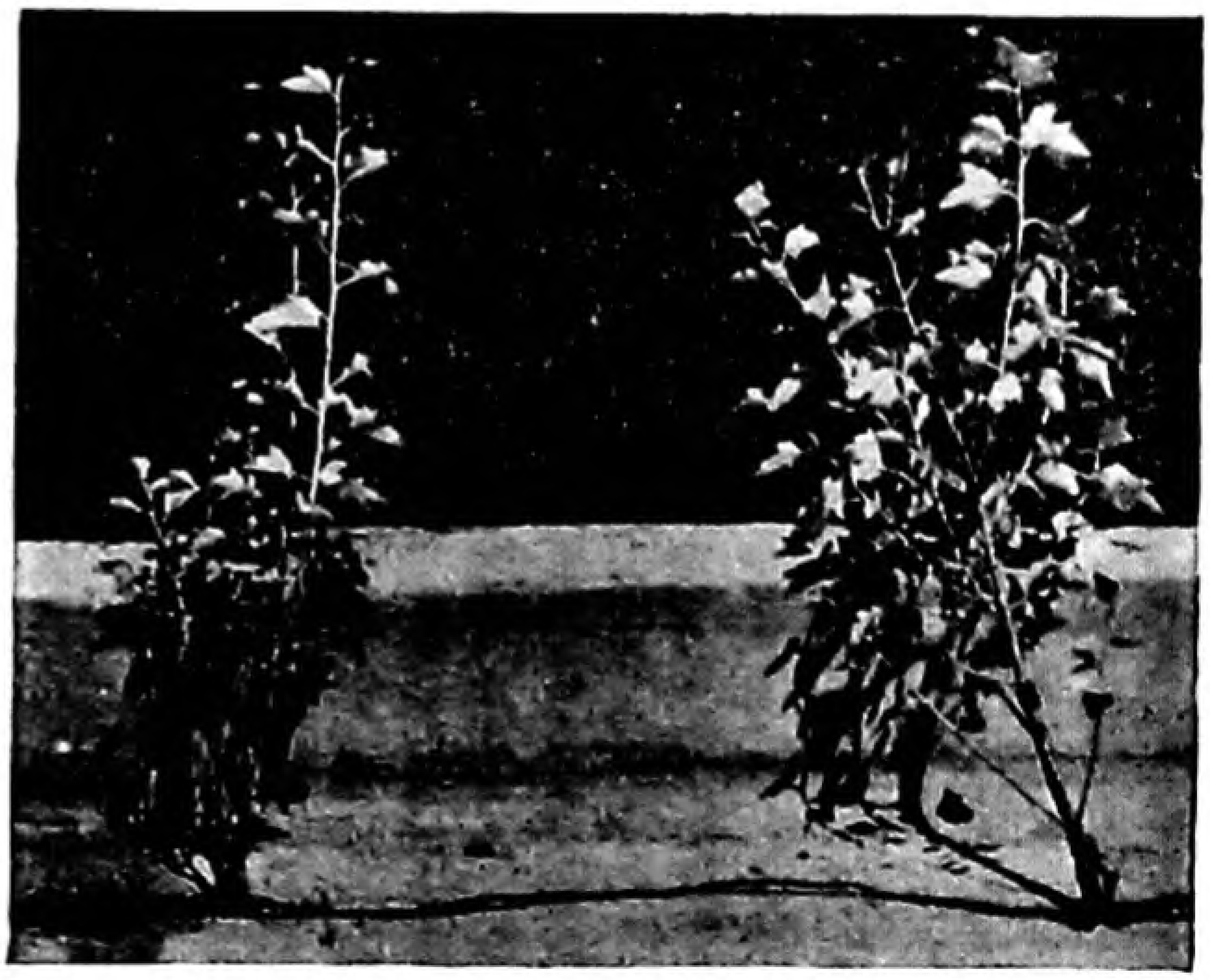
A short distance below the tip is a series of protuberances which are the beginnings of leaves, or *leaf primordia*. In the axils of the older ones of these, the lateral buds are beginning to appear in the form of meristematic enlargements. These leaves and buds mark the first appearance of nodes.

Somewhat below the apex, in the region of elongation, many of the cells are larger, their protoplasm is less dense, and differentiation into a considerable number of types of tissues is taking place. One of the most important of these—because of the roles it plays—is the *procambium*. In prepared slides of longitudinal sections this tissue can be easily recognized as a narrow strip of deeply stained cells a short distance toward the center from the epidermis. Careful examination shows these cells to be considerably lengthened up and down the stem. In the somewhat older parts where the region of elongation is ending and mature tissues are organizing, the innermost procambium cells become changed. Their walls develop spiral and annular thickenings after which they are no longer meristem, but *primary xylem*. At about this time the end walls between them disappear, the protoplasm vanishes, and they have become true mature vessels.

At about the same time the outer layers of the procambium become transformed into *primary phloem*, and between the phloem and the xylem there remains a narrow zone of meristematic cells, the *cambium*. At this level, near the lower, older part of the region of elongation, the tissues of the entire stem including epidermis, cortex, and stele with the exception of cambium, are mature and permanent, all descended from the apical meristem. These are the *primary permanent tissues*. The cambium is the only meristem remaining, and its products are *secondary xylem*, *secondary phloem*, and *secondary rays*, as contrasted with the primary tissues from the apical meristem.

How Buds Organize. Embryonic leaves begin to take form just behind the apical meristem. As they develop somewhat, they enwrap the growing tip, forming the terminal bud. A little later, similar masses of meristem develop in the axil of each young leaf around which leaf primordia soon become organized. These meristems with their wrappings become the lateral buds. The lateral buds assume the same positions on the stem as the leaves in whose axils they form. In other words, buds as well as leaves may be opposite or alternate.

When the terminal bud continues to grow it causes the stem of which it is a part to increase in length, while the growth of lateral buds results in the production of branches. Under certain conditions, a part or all of the buds of many plants remain inactive for longer or shorter periods of time.



Shoots of white poplar arising adventitiously from horizontal root.

The situation described above is the usual one. Under some circumstances, however, *adventitious*

buds may arise. These are not in the axils of leaves and are not located at nodes. In fact, almost any living, unspecialized tissue or meristem such as cambium or the various parenchymas may organize them. Adventitious buds and the stems developing from them may often be seen on stumps of trees that have been cut down, and on large roots of such woody plants as plum, Osage orange, sumac or white poplar, to mention only a few of the numerous examples.

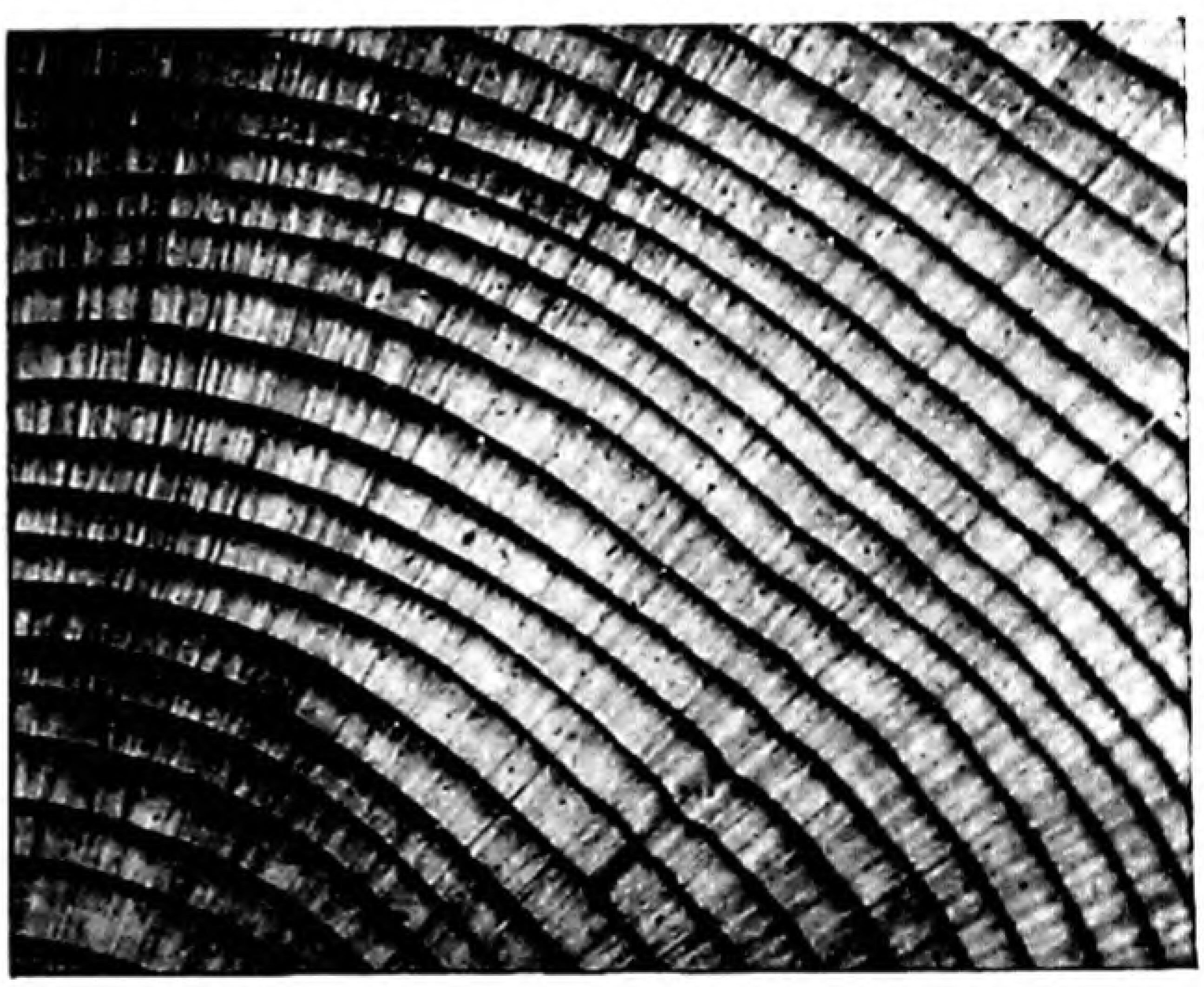
It should be understood that leaves can be formed only from a growing tip. If they sometimes seem to arise from the side of a mature stem or from some other unusual place, a close examination will show that they really come from an apical meristem of a short, lateral branch or else from an adventitious bud.

Older Dicotyledon Stems. Thus far root and stem anatomy in young dicotyledons, or in those in which the cambium is more or less inactive, have been studied. In other words, little more than primary tissues have been examined. But in many plants cambium produces considerable amounts of secondary xylem and phloem, and cork cambium builds the corky outer layers of the bark. Cambial activity increases the diameter of the roots and stems in which such growth occurs.

GROWTH IN THICKNESS. Cambium is regularly present in the roots and stems of most dicotyledons. In trees, shrubs, and many herbs, its activity continues indefinitely and the plant body therefore increases in diameter. In many other plants it becomes quiescent after a short time. This is the reason why melon and pumpkin vines reach their maximum thickness in a few weeks after they are formed, and remain slender and uniform in diameter throughout most of their length. The same is true of such specialized stems as the runners of the strawberry and the rhizomes of many species. Merely having a cambium does not prove that a stem is certain to continue to grow in diameter, for cambium, though present, may remain or become inactive.

HOW CAMBIUM PRODUCES SECONDARY TISSUES. Cambium cells are usually long and slender, extending lengthwise in the stem, forming a delicate sheet along the outer surface of the xylem, separating it from the phloem. During periods of active growth, cambium cells divide lengthwise by mitotic divisions. A part of the daughter cells retain their meristematic character and continue to be cambium, while the remainder become specialized. Those that form on the side toward the xylem, organize into xylem cells while those on the phloem side produce phloem. The changes from cambium to mature secondary tissues require a considerable period of time. The amount seems to depend largely on weather and climatic conditions. It is safe to assume that at least several days are required even in plants that are producing secondary tissues very rapidly.

The youngest of these differentiating cells, which are nearest to the cambium, cannot be readily distinguished from the meristem itself, while the older ones gradually merge into the mature xylem and phloem. The cambium proper is composed of one or a very few layers of meristematic cells, but that tissue, together with the immature secondary ones arising from it, may often be seen in sections of stems and roots as a rather thick band of thin-walled cells.



Growth rings in pine wood. The lighter part of each ring was formed in spring and early summer; the dark layer of very dense wood organized in late summer. Note the clear-cut, sharp line separating adjoining growth rings.

GROWTH RINGS. Growth rings are the layers of wood laid down by the cambium in successive periods. As seen in cross sections of stems or roots

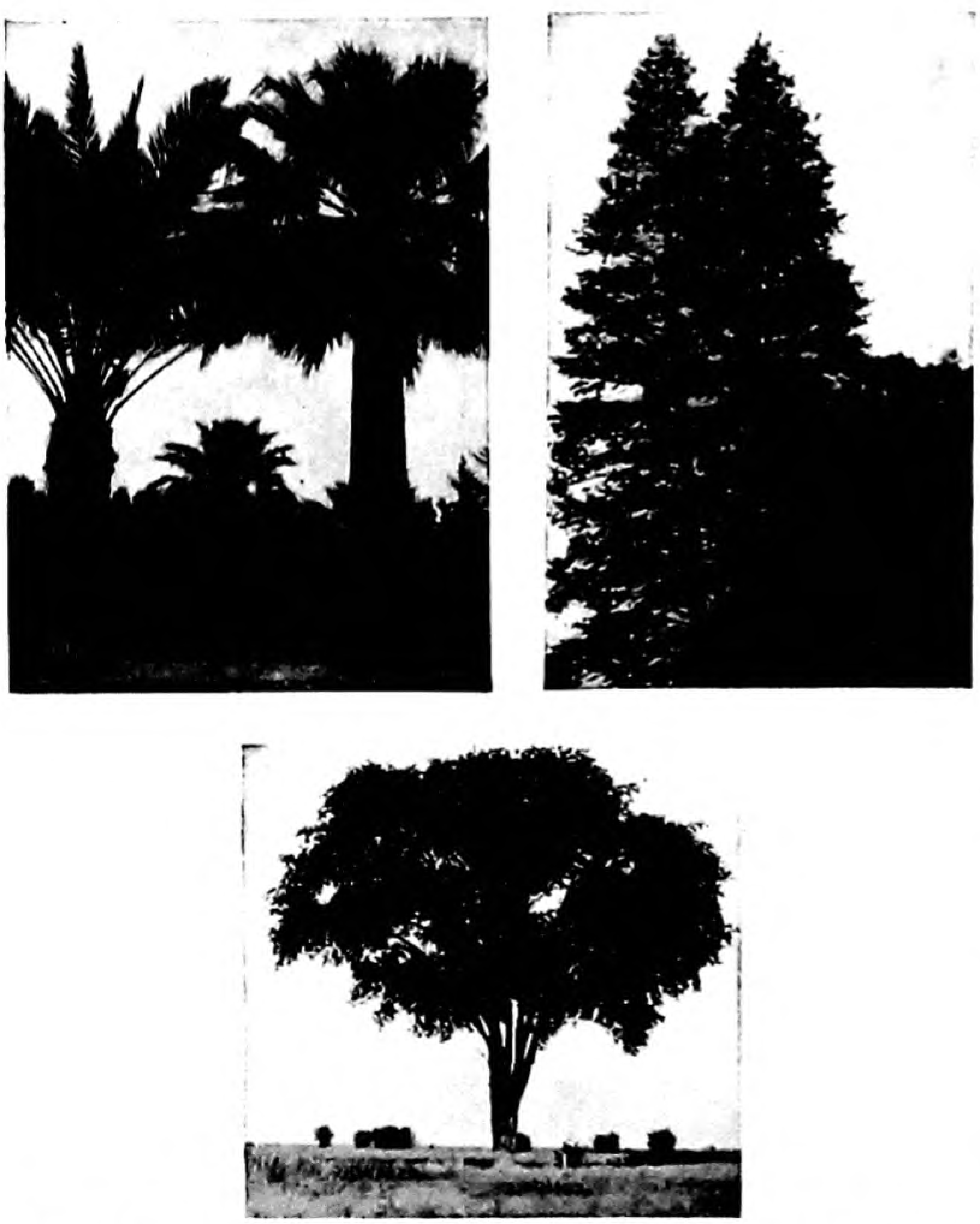
they appear to be rings, but actually they are woody coatings over the entire outer surface of the xylem. During each growing season the apical meristem adds somewhat to the length of the stem while the cambium adds a layer of wood to its diameter.

Growth rings are limited chiefly to the woody stems and roots of dicotyledons and gymnosperms. They are formed in the following manner: At the beginning of growth in the spring large conductive tubes are formed. Later in the season smaller cells develop and by midsummer the cambium ceases or almost ceases to produce more xylem. The spring and summer wood, therefore, commonly constitute a season's growth, or a *growth ring.* Each year the wood with large vessels that form in the spring grows attached to the dense summer wood of the previous year, thus making a visible line between the layers produced in successive growing seasons.

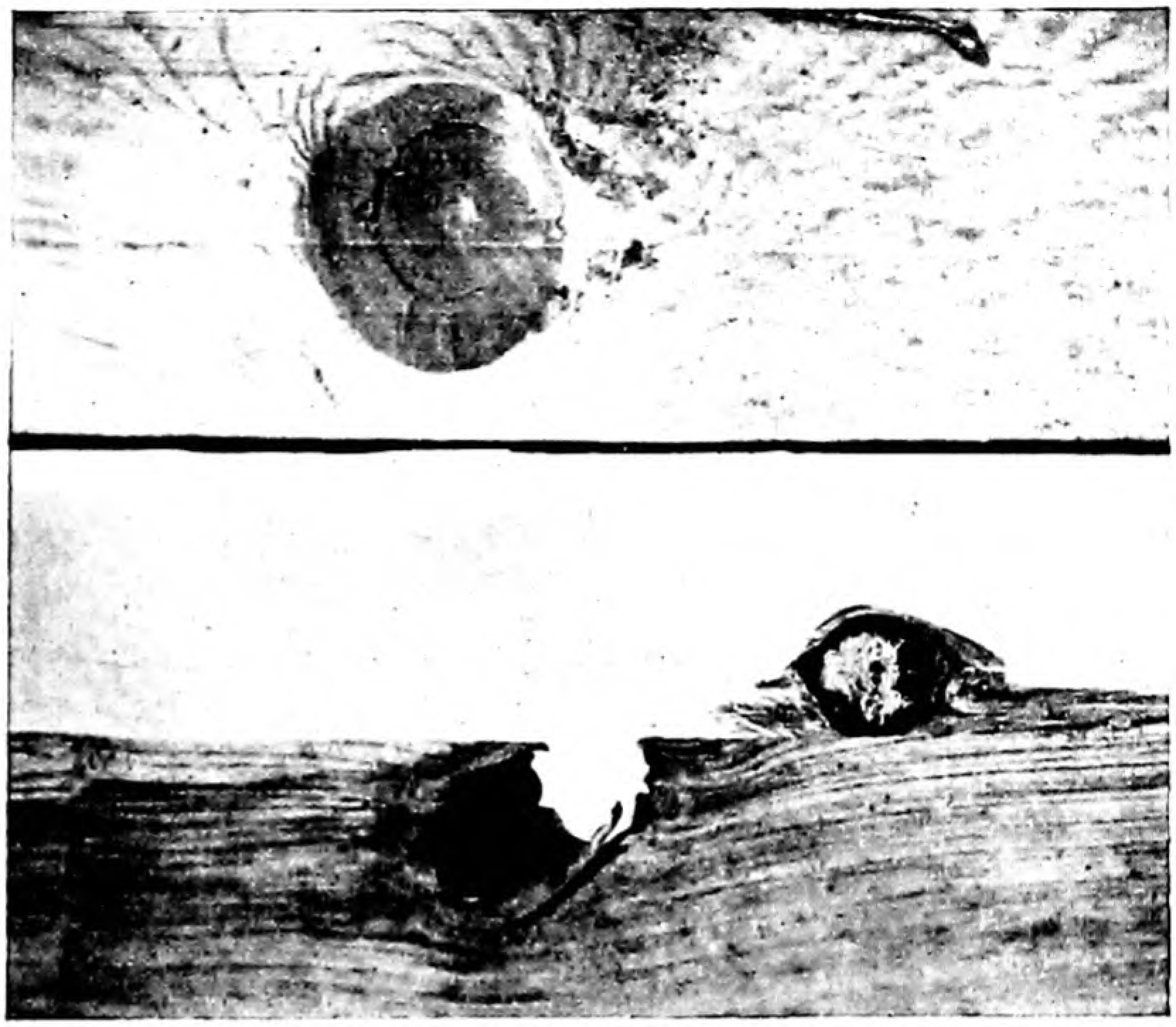
All these statements apply to the usual situations. For this reason it has been customary to say that by counting growth rings with great care the exact age of a log or stump can be determined, but this statement is not always entirely accurate. Two situations are known to bring about the production of more than one ring in a growing season. For some time it has been known that when actively growing leaves are all removed from trees, as when they are destroyed by a severe hail storm or are devoured by insect pests, dense wood is produced in the stems, in this way completing a growth ring. If, as often occurs, a new crop of leaves develops, cambium may resume its activity and the spring type of wood is organized. With the end of the season dense wood is again formed furnishing a second growth ring.

A second condition under which additional growth rings may develop has been discovered recently. Investigations still in progress, in which the behavior of cambium and its products are being followed with great precision, are showing that under sharply fluctuating weather conditions, more than one and sometimes several clear rings may be produced during a single season. These rings are often so definite that no way has been devised by which to distinguish them from true annual rings even with a microscope.

In the light of these facts it is evident that counting growth rings gives only a fair approximation of the exact age of a tree. Nevertheless, under the climatic conditions that prevail over large areas of the country such age determinations are probably very nearly correct.



Tree forms. (*Top, left*) Columnar trunks of palms. (*Top, right*) Excurrent branching of Douglas firs. (*Bottom*) Deliquescent branching of American elm.



Knots in lumber. (*Top*) Live knot. (*Bottom*) Dead knot and knot hole.

Numerous investigations that have been in progress during recent years have shown conclusively that growth rings vary greatly in thickness under different amounts of rainfall. So responsive are the rings of some trees to available water that they are a fairly reliable record of conditions in the year in which they grew. As an example, during a recent year of drought, a grove of western yellow pines growing on a high rocky ridge in one of the Southwestern States, did not receive enough rain during the entire spring and summer to moisten the soil to the depth of even the shallowest roots. The growth rings produced by these trees during that season were only five or six cells in thickness. These rings were so thin that they could not be recognized except with the microscope. During that same season other similar trees growing in continuously moist soil because they were near a spring, added growth rings from 60 to 70 cells thick. Since these two sets of trees were only two miles apart it seems certain that the difference is to be attributed solely to differences in available soil water.

Working on the assumption that growth rings give reliable records of past weather conditions, a fascinating study of tree rings and climatic conditions in the past is being worked out in some of the more arid regions of this country. By this same study it is thought that the erection dates of certain prehistoric buildings can be determined. Growth rings in ancient logs, and even pieces of charcoal, have been dated with a fair degree of accuracy, making a continuous, overlapping record that reaches back at least to the beginning of the Christian Era.

On the other hand, some woody plants have no growth rings. This is characteristic of the giant cactus of southern Arizona and portions of neighboring states. This great fleshy tree often grows to be forty feet tall and some specimens are said to attain a height of sixty feet. The xylem forms as a dissected cylinder around a gigantic central pith several inches in diameter. The cortex is also extremely thick. Almost the entire plant with the exception of the xylem is a mass of water and food storage tissues.

Rainfall in this section of the Southwest varies remarkably from season to season and from year to year. For this reason, by comparison with other woody plants, one would expect both wide and very narrow growth rings, corresponding with the wet and dry seasons or years. Instead, there are no traces of ring formation, for the wood is uniform throughout. The explanation seems to be that the great supply of water held in the tissues at all times provides a continuous source, permitting the various growth processes to proceed slowly throughout the years without regard to periods of rainfall and drought. Whenever there is ample rainfall these giant living cisterns become filled with imbibed water in sufficient amounts to supply all needs for many months to come. So independent are these great fleshy trees of supplies of soil water that they sometimes blossom freely and ripen fruit with their roots embedded in soil as dry as dust.

Because the wood of these trees gives no hint of the number of years they have grown, the only way yet devised to discover their approximate ages is to measure rates of growth in height and diameter and to make estimates from these. Such a procedure is obviously very unreliable, but the biggest trees are considered to be two or three hundred years old.

FORMS OF TREE TRUNKS. Tree trunks take three rather distinct shapes. Sometimes they are entirely unbranched, assuming the *columnar* form with a crown of leaves at the top. Palm trees and some of the cycads are the best examples of this type. The next more complicated forms are trees with *excurrent branching* (*excurrere*, to run out). This type has a main upright trunk from which smaller branches extend outward with the shortest at the top. This arrangement gives the tree a conelike shape. Spruces, firs, hemlocks, some of the pines and other cone-bearing evergreens as well as such deciduous forms as beech trees and aspens are good examples of this type.

The remaining type is *deliquescent* branching (*deliquescere*, to dissolve gradually). Here the main trunk extends upward for only a relatively short distance before it gives place to large branches that frequently do not grow in a vertical direction. These divide and subdivide until their ultimate ramifications are the smallest twigs. Such round-topped trees as apples, elms, and old cottonwoods have this type of branching. Some trees, as the sugar maple, have excurrent branching when they grow in close stands but become deliquescent when not crowded.

NATURAL PRUNING. Young twigs whose leaves are so placed that they receive insufficient sunlight soon starve, die, and drop off. This kind of action is called *natural pruning*. Under the canopy of leaves of a dense forest a great majority of the young shoots that arise along the tree trunks are eliminated in this manner, and even large branches that have started to develop in ample light, may die if they become deeply shaded.

KNOTS. Whenever lateral buds grow in length they form branches. The cambium and growth rings of these and of the main shoot are continuous. As a result, the base of every branch becomes more deeply embedded as, year after year, new layers of wood are formed. It is these embedded branches that take the form of knots in logs and in sawn lumber. Knots that are formed by living, growing branches are commonly firmly attached to the surrounding wood. On the other hand, dead branches, having no active cambium of their own, become surrounded by living wood but are not a part of it. Those formed in this way, commonly called "dead knots," frequently drop out of lumber, leaving holes.

DEVELOPMENT OF BARK. During the early part of the season in which they are produced, young twigs are usually green because the transparent epidermis allows the chlorophyll in the underlying tissues to show through. By the end of the first growing season, or in some instances, a few years later, the epidermis is likely to be replaced by a gray or brown corky layer of outer bark, which partly obscures the green color. Successively older segments are often clearly distinguishable by the differences in color due to

Twig of box elder showing changes in bark with increasing age.

Bark of trees. (*Left*) Shag-bark hickory. (*Center*) One-seeded juniper. (*Right*) White oak.

the degree of development of this layer of cork.

Cork is produced by a special tissue, the *cork cambium*, which makes its appearance beneath the epidermis, usually while the stem is still young. It arises from the parenchyma or the collenchyma, or occasionally, by the division of epidermal cells.

As the new cells mature, their walls are reinforced with a thin, uniform layer of *suberin*, a mixture of substances much like ordinary fats or waxes. Suberized walls are comparatively impervious to water. For this reason all tissues outside the cork are effectively cut off from supplies of both water and food. Therefore, the epidermis and any parts of the cortex beyond the corky layer quickly die. At the same time the underlying tissues are protected from drying.

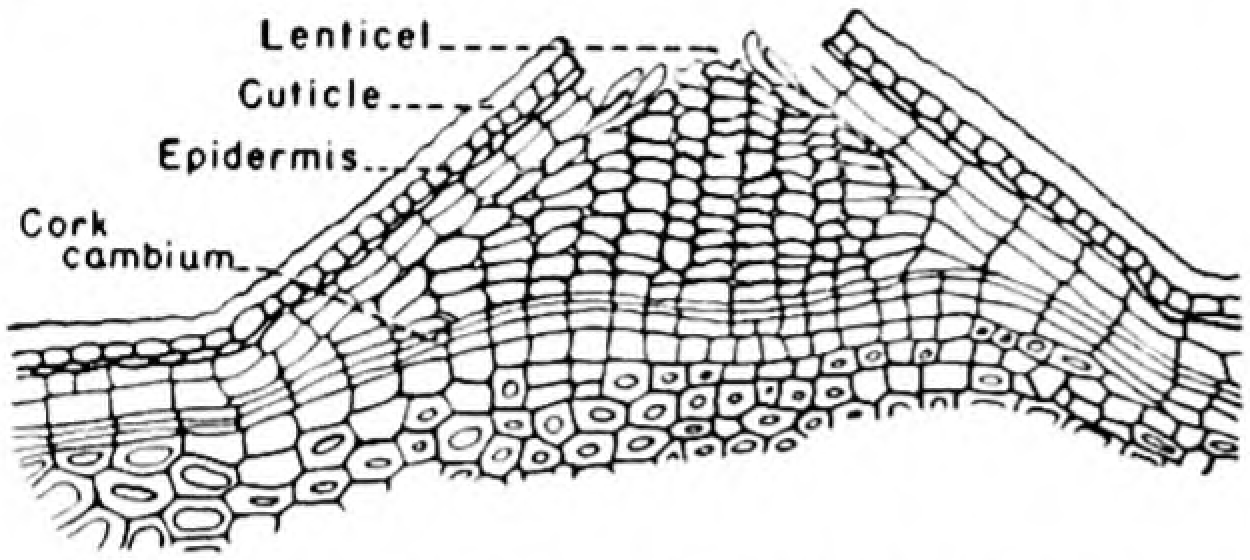
When the cork cells are produced only on the outside of the cork cambium, they may be added, layer after layer almost indefinitely, without complication; but if, as occurs in some species, a layer also forms on the inner surface of the cork cambium, the latter is in time shut away from its own supply of food and water and its activity comes to an end. When this happens, another cambium comes into existence deeper in the cortex or even the phloem parenchyma may organize a cork cambium. (See p. 107.)

As the stem grows larger, the cork layer is stretched, and finally the outer, harder, part splits or breaks, the cambium continuing all the while to make new layers that fit the circumference. The rate of growth of the cork, its thickness and texture, and the nature of the overlapping layers are so effective in determining the way in which the bark will break and so characteristic of each species of tree, that the appearance of the outer bark of their mature trunks is an important aid in identifying many trees.

As examples, the outer bark of shag-bark hickory (*Carya ovata*) is in the form of hard, almost dagger-like strips; that of the various oaks is hard, furrowed, and rough; and of most of the junipers is stringy or shreddy. The white bark of sycamores

(*Plantanus*) sheds in the form of thin brittle patches; of the aspens as a chalky dust, and of birch trees as more or less papery layers.

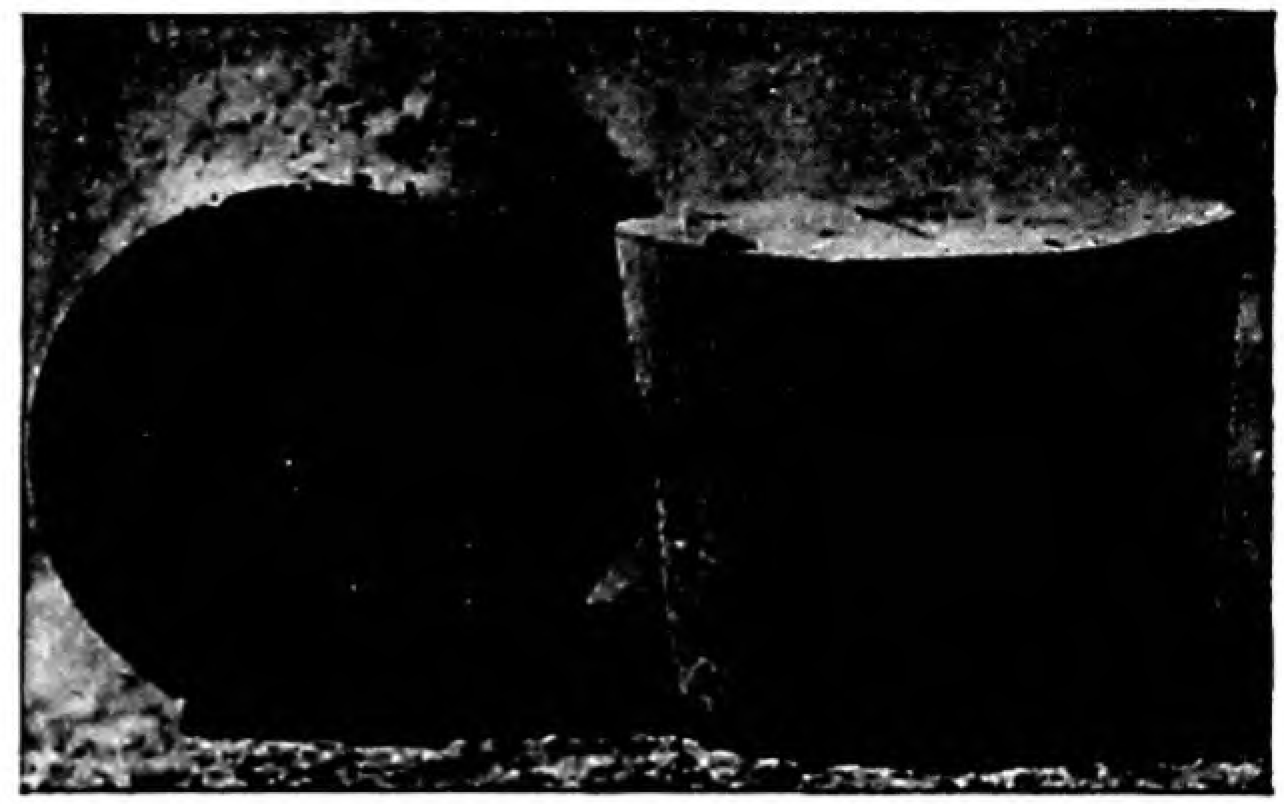
LENTICELS. Examination of a twig or well-developed root of almost any woody plant reveals nu-



Section through young lenticel of elderberry.

merous small, scattered, wartlike enlargements. These are the *lenticels*. The very youngest parts of the twigs have a covering of epidermis with stomata much like those of leaves. As the stem grows somewhat older and larger in diameter and the epidermis begins to be replaced by cork, the

Lenticels of yellow birch, that have become greatly enlongated around tree trunk as the tree has grown in circumference.



Lenticels seen as porous tubes in cross and longitudinal sections in bottle corks.

lenticels take form. They organize under stomata and replace them both in position and in function when the epidermis disappears, acting as ventilating organs for the internal tissues.

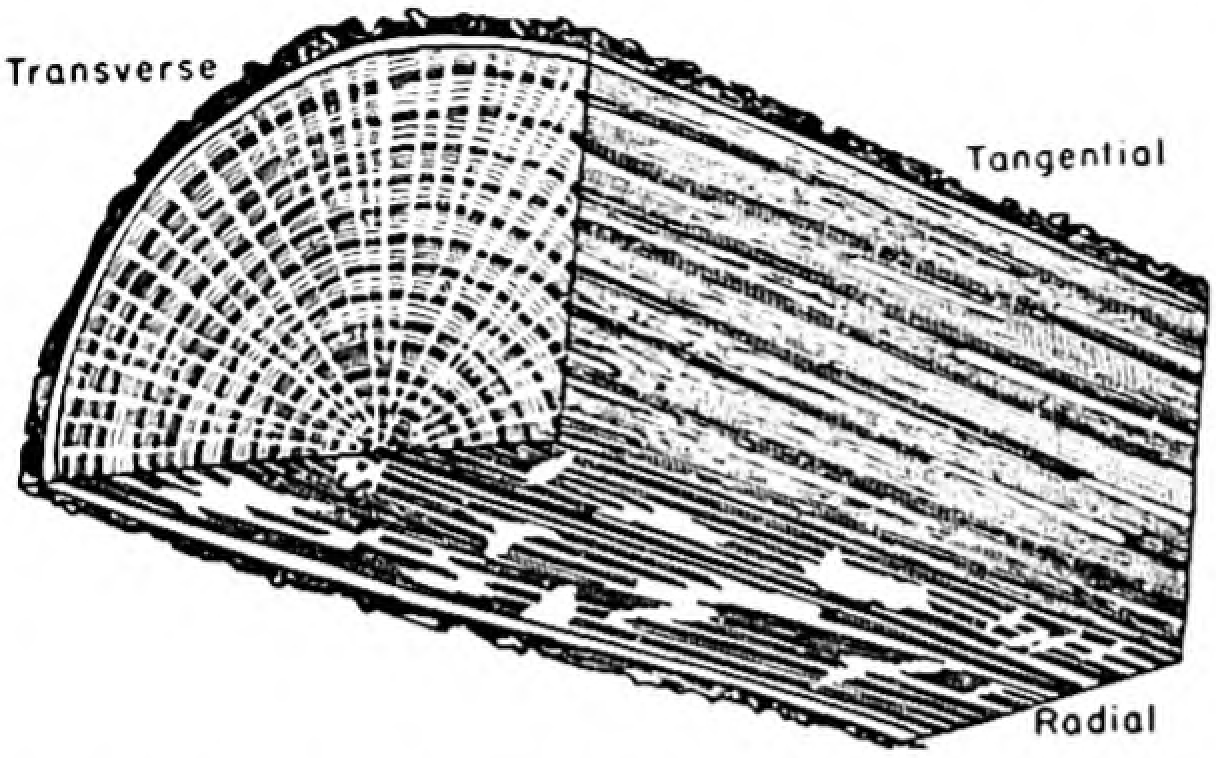
In the case of old tree trunks with rough bark, lenticels, although present, are frequently difficult or even impossible to see. In contrast, they show clearly in the smooth bark of such trees as birch, plum, and cherry. In these the bark continues to live and grow for a considerable number of years, gradually extending as the diameter of the trunk increases. The lenticels therefore become greatly elongated around the stem.

In the outer bark of most trees the true cork cells are associated with fibers, sclereids, and fragments of other tissues to such an extent that the result is a coarse, brittle layer of such heterogeneous nature that it does not lend itself well to any important use. One species of tree, the cork oak (*Quercus suber*) of Southern and Western Europe, has a cork layer which is so fine-grained and uniform that it furnishes all of the commercial supply of this commodity. By making shallow cuts around the trunks of these trees it is possible to remove the cork in large sheets without injuring the underlying tissues. In a few years the cork cambium has produced another layer, and another crop can be harvested.

A piece of cork is a mass of cubical or rectangular cells with no living contents. The comparatively thin, suberized cell walls are elastic and waterproof, and the large cell cavities make the tissue light in weight. A little thought about the many uses of

cork will suggest a close correlation between its economic value and its microscopic character.

An examination of a large bottle cork shows numerous spongy tubes extending across it. These are the lenticels. If they extended lengthwise through



Block of oak wood showing growth rings and rays in transverse, radial, and tangential sections. In a longer block the growth rings in tangential section take on elliptical forms.

the stopper it would have little value in preventing the evaporation of liquids. For this reason the manufacturer must cut the bottle corks in such a way that their ends are parallel with the surface of the sheet.

THE STRUCTURE OF WOOD. To have a working understanding of wood structure one needs to study a block cut from a small tree in such a way that certain definite relationships are made clear. To this end a *transverse section* should first be examined. This is made by cutting directly across the stem. The most obvious lines seen are the growth rings encircling the central pith and the rays squarely crossing them.

If, next, the surface made by cutting the stem lengthwise through the central pith is examined, it becomes evident that the plain of cleavage follows the rays. This is called a *radial section*. Again the growth rings and the rays are seen, but in a very different perspective. From this point of view it is easy to understand that those structures that are commonly called rings when they are seen in cross section of the stem are actually layers of wood. In the radial section these layers appear as almost parallel lines running vertically through the block. The rays in this section are laid bare, extending across the growth layers in the form of larger and smaller flecks and patches.

A final angle of observation is had by making a lengthwise cut at some distance from the central pith and at right angles to a radius and therefore tangent to growth rings. This is called a *tangential section*. In this section the ends of the rays are cut across and the growth rings show as broad irregular, more or less elliptical lines or bands.

Reference to the illustration above or better still to any block of wood cut along these lines should make clear the relationships of the various parts. With a little practice it should become possible for the student to recognize these different sections as seen in such wood work and furniture as may be at hand. To interpret any block of wood the student should keep clearly in mind the facts that the rays always squarely cross the growth rings and extend away from the central pith. These relationships can be recognized even in lumber that has been cut from the outer parts of logs, and, therefore, does not include the central pith.

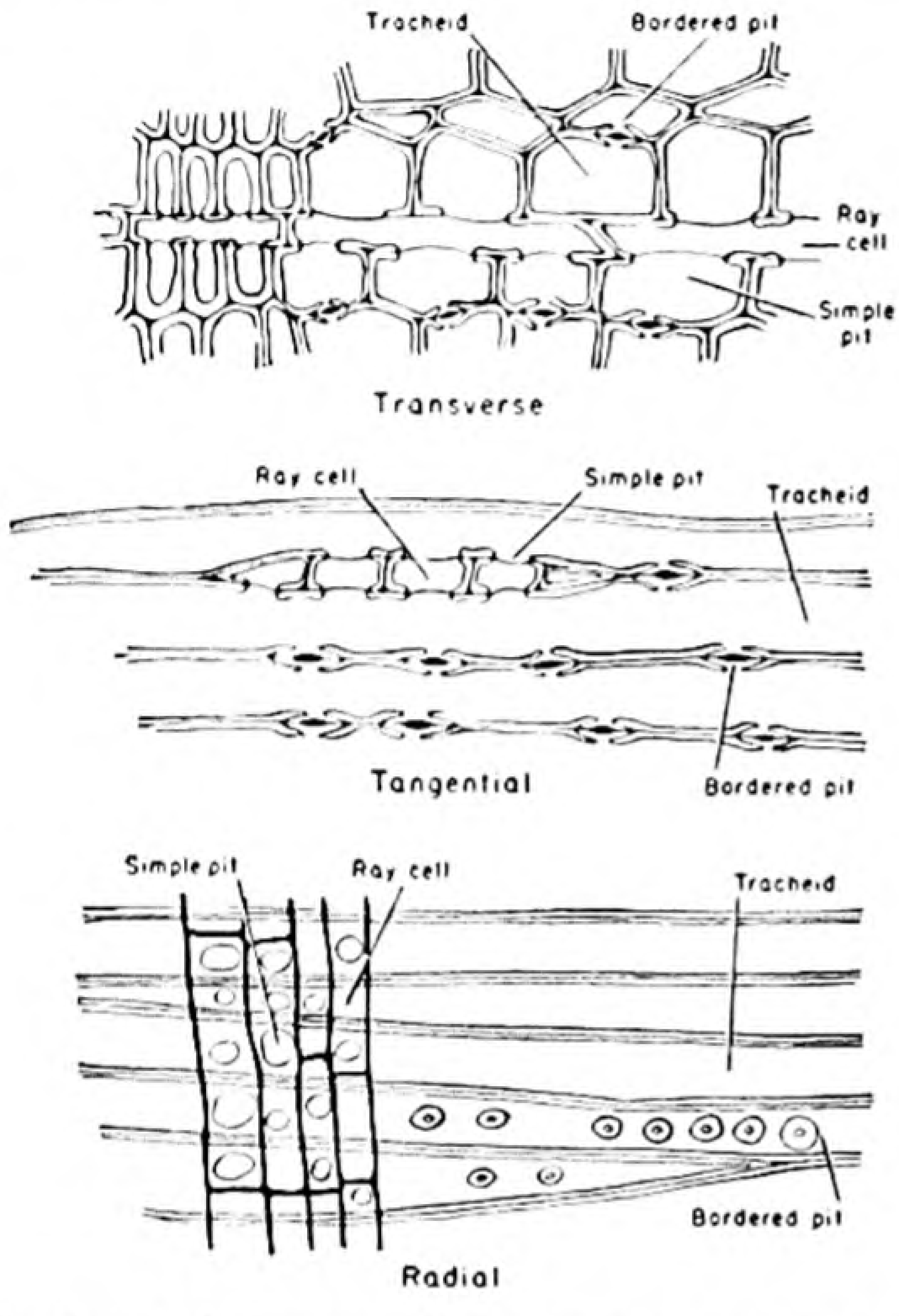
When the relative positions of these parts and their appearance from different directions have been mastered, an examination of the cells as seen in thin section with the microscope should be undertaken.

The wood of pine is relatively simple and therefore easy to interpret. Aside from occasional *resin ducts* lined with glandular cells there are only the tracheids and rays. In transverse sections the tracheids occur in more or less regular rows in both directions and at certain places the demarkations between two growth rings stand out sharply. The rays can be recognized as lines of cells extending at right angles to the growth rings.

In the radial section the tracheids can usually be identified by their relatively thick walls while the thinner-walled rays extend across them, the entire group reminding one of the crossings of numerous railroad tracks. The tangential section is much like the radial except that the rays are cut transversely, having the appearance of small groups of cells crowded in between the tracheids.

In contrast with pine, the wood of oak is very complex. In addition to tracheids there are both wood fibers and numerous large vessels. Probably

the most confusing part to the person first examining this wood is the rays. Their walls are all very thick and highly lignified. Some of the rays are *simple*, that is, one cell thick, but many are *compound* and very wide.

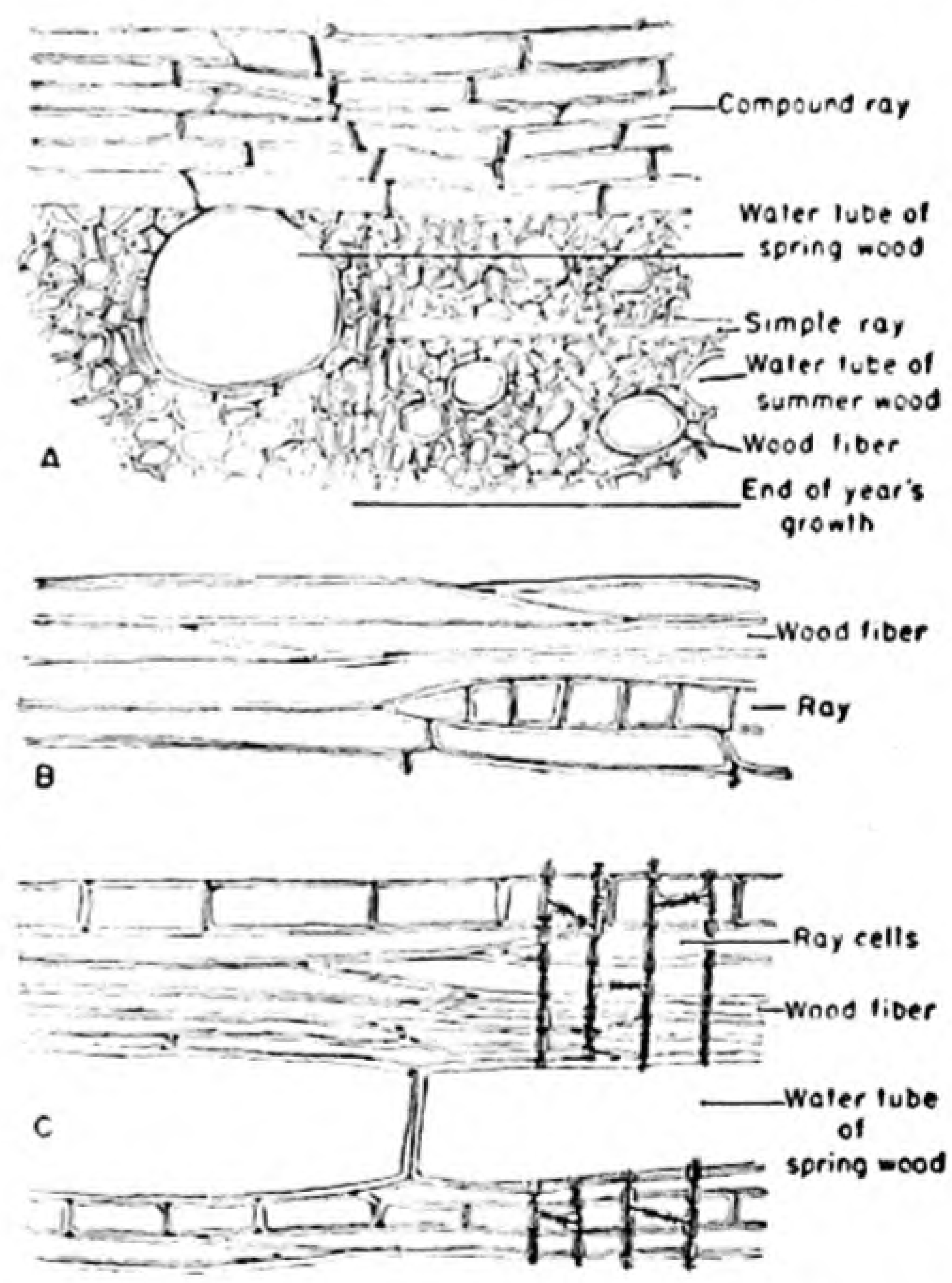


Sections of pine wood as seen with the microscope.

PITS. Whether in gymnosperms or angiosperms, all tracheids and vessels of the xylem have *pits* in their walls. These are holes or thin places where there was little or no deposit of lignin. They may occur at almost any place where the sides of two conductive tubes touch one another or where a vessel or tracheid is in contact with a ray cell. In the radial walls of the tracheids of pine there are many elaborate *bordered pits* with peculiar overhanging extensions. It is difficult to describe these in words, but some idea of their appearance can be obtained by studying the illustration above. Those in the wood of dicotyledons are commonly *simple pits*, that is, they have straight instead of overhanging sides.

HEARTWOOD AND SAPWOOD. After the trunk and older roots of many trees have grown for several years the innermost xylem cells become clogged with various gums, resins, dyes, and other substances, stopping the flow of water through the conductive tubes. These materials usually give the wood a darker color, often making it contrast sharply in appearance with the light outer parts. This dark inner portion is called *heartwood* and the outer newer part where the vessels and tracheids are still open and functional is called *sapwood*. Heartwood seems to be of little value to a tree aside from the mechanical strength it contributes. That it is not necessary to the effective transfer of materials through a stem is shown by the fact that trees often live for many years after the heartwood has been completely destroyed by decay, leaving the trunk hollow.

GRAIN. The kinds of tracheids, vessels, fibers, parenchyma cells, and rays, together with their arrangements, determine the texture, or *grain*, of wood. Grain is important in the appearance of



Sections of oak wood. (A) Transverse. (B) Tangential. (C) Radial.

furniture and in both the appearance and wearing qualities of floors.

A knowledge of wood structure makes it possible to cut it in such ways as to expose the grain to best advantage. Boards cut parallel to the radius of

a log expose the edges of the annual rings. Such lumber wears well under hard usage, as in floors, because of the narrow alternating hard and soft strips which make up the parts of the growth rings. Those cut at right angles to the radius, that is, tangentially, expose much wider alternating strips and do not wear evenly. When oak wood is cut parallel to a radius, the prominent lignified compound rays are exposed in irregular areas, sometimes called "silver grain," giving a very fine appearance when properly polished. Since a log is first sawed radially into four quarters when this type of cut is to be made, this lumber is known as "quarter sawed oak."

Growth in Length of Roots and Stems. It is ordinarily only at the growing tip of the stem that new nodes and internodes can be formed. Likewise, roots elongate only at their outer extremities. Measurements show that increase in length in both roots and stems occurs most rapidly immediately behind the growing tip, the amount of increase becoming less and less until finally there is none at all behind the region of elongation.

Fully matured portions of stems, like the trunks of trees, do not grow in length. There are some erroneous ideas on this subject, but a few years of observation on marked trees, with careful measurements and complete written records each year, should convince anyone that tree trunks do not extend in length. It is true that small trees often have branches all the way to the ground and older ones have their trunks bare below, but this is the result of the dying of the lower branches and the development of new ones above, and not of the bodily uplift of the whole tree top. The knotty texture of the wood in the middle of the log, as revealed by the sawmill, is further evidence of this fact.

Certain definitely jointed stems, like those of the grasses and mints, behave in a somewhat different manner. They grow in length in the usual way at the tip; in addition, each internode as it develops matures from the top downward and retains at its lower end, just above the next node, a small segment of embryonic tissue, called *intercallary meristem*, by means of which it continues to lengthen. In this way a cornstalk sometimes increases tenfold in length after all its internodes have been formed; or the stems of some lilies grow three or four inches in a day, and those of bamboo add more than three feet to their height in a single day. All of these have this type of growth mechanism.

When this great ability to increase in length occurs in a stem which has no way of growing in diameter, as is the case in many of the monocotyledons, the result is a very long and slender stem. If the trunks of some of the California redwood trees were as long in proportion to their diameters as is a well-developed rye straw, the trees would be about two miles tall.

Oak log showing dark heartwood and light sapwood.

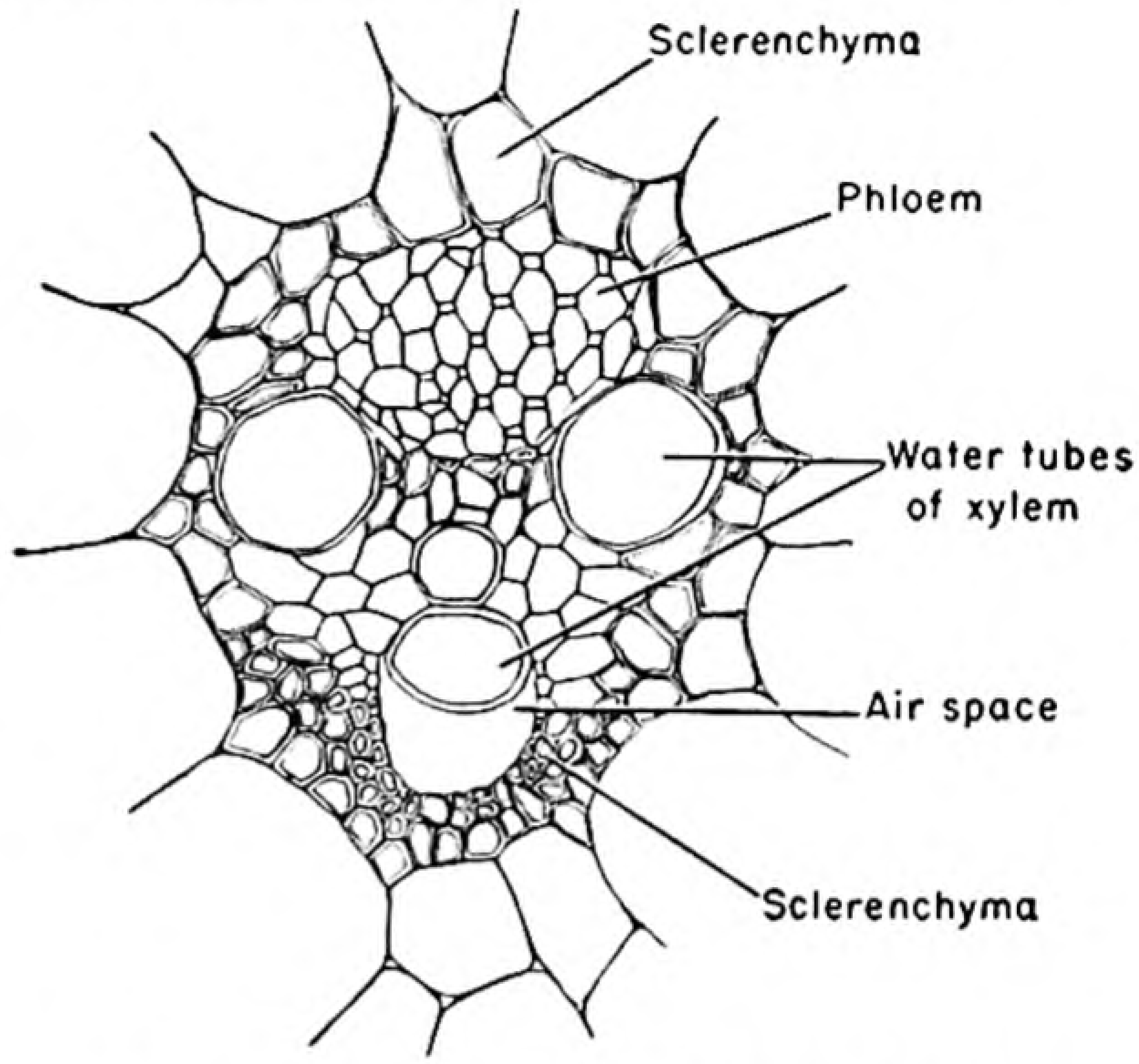
The Scattered Stele of Monocotyledons. ORGANIZATION. The stem of either a typical dicotyledon or of a gymnosperm contains a siphonostele. In contrast, that of a monocotyledon almost always has a *scattered stele*. That is to say, the monocotyledon stem usually has no definite central pith, the stele is very much dissected, and the vascular bundles are scattered irregularly throughout a general background of pithlike tissues. This type is very well shown in the various grasses, sedges, lilies, palm trees, yuccas, and in fact in almost all monocotyledons. In some cases, as

in most of the grasses, the stem is hollow, but even in these the bundles are distributed irregularly through the tissues.

A careful dissection of a few internodes of such a stem of a monocotyledon as a cornstalk made in such a way as to trace the vascular bundles, shows the reason why they are scattered as seen in cross section. The reason is shown to be that they do not extend exactly parallel with each other, but wander more or less throughout all parts of the pithy tissue, and that they anastomose and redivide at the nodes.

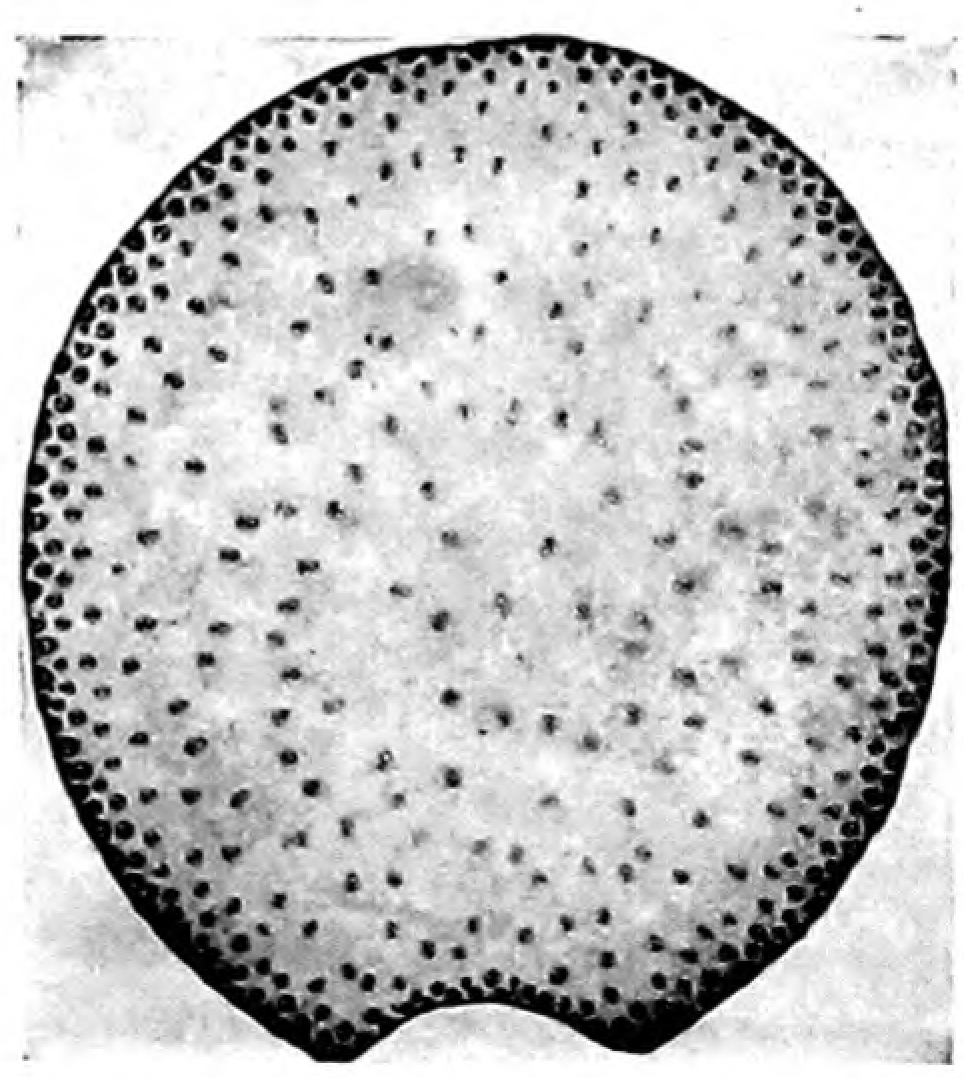
Thin sections cut transversely across a corn stem, and properly prepared for study with the microscope, reveal several important features. The vascular bundles are scattered through the section without much system in their arrangement, those near the epidermis being smaller and more crowded than those in the center. Except for a layer of fibrous or woody cells next to the epidermis and, sometimes, a sheath of fibers around each bundle, the space between the bundles is filled with large, thin-walled, loosely arranged cells of pith.

In the various other monocotyledons the vascular bundles are much the same as in corn. Each has one strand of xylem made up of a few vessels together with some fibers, and one of phloem composed of sieve tubes and companion cells. The phloem has a tendency to be turned outward toward the epidermis. There is either no cambium or at most a short-lived one, and as a consequence the bundles have no way of becoming any larger after they have formed and their original cells have reached their full size.



Cross section of vascular bundle of corn.

There is no visible endodermis in the corn stem and no differentiation into stele and cortex. In some palm trees, however, as well as in the stem of the greenbrier (*Smilax*) and in the rhizomes of certain related plants, in all of which the stem is otherwise much like that of corn, there is a more or



Scattered steles of monocotyledons. (*Left*) Part of cut end of trunk of palm tree. (*Right*) Cross section of corn stalk, somewhat magnified.

less definite cortex and sometimes a rudimentary endodermis.

The vascular anatomy of these plants has been interpreted in several ways, but their stems may be thought of as having steles which have become completely dissected and then had the resulting bundles disarranged. In fact just this action occurs in the development of a young plant of this type. A transverse section through an internode of a corn seedling where it is emerging from the grain, shows the young stem to be a siphonostele, while a few internodes higher on the stem, the stele has become scattered.

It is possible, now, to summarize the types of steles of stems of the seed plants by saying that, with slight exceptions, gymnosperms have continuous siphonosteles, dicotyledons have continuous or dissected siphonosteles, and monocotyledons have scattered steles.

THE ORIGIN OF VASCULAR BUNDLES IN MONOCOTYLEDONS. As in other seed plants, the youngest part of the stem tip of a monocotyledon is an apical meristem. In most respects it is similar to the meristematic tips of other plants but in the region where tissues begin to differentiate the procambium becomes organized, not as a more or less well-formed layer but as numerous scattered strands, each of which soon changes into the primary xylem and the primary phloem of the bundles.

Although it is difficult to make general statements about the varied collection of plants which make up the monocotyledons, it is true that none of them has an active cambium of the dicotyledon type, although a few have cambial cells which may divide a few times. Some of the larger monocotyledons, however, have a peculiar cambiumlike tissue which is well illustrated in some species of palms and in some of the yuccas and century plants. When the stems are first formed they are much like that of corn except that they have a cortical region of parenchyma without vascular tissue. A short distance outside the vascular region certain cells of this cortex now begin to grow and divide like those of cambium. They do not, however, form new xylem and phloem as do ordinary cambium cells. Toward the exterior they form a protective layer of cork and on the inside a layer of parenchyma traversed lengthwise by a system of intercommunicating vascular bundles.

Summary. The stem has a primary function of displaying leaves to the light where photosynthesis can occur in an efficient manner. A secondary function is the bringing of water to the leaves and the return of foods and growth substances to the roots and other parts of the plant. The conductive activities are chiefly centered in the stele. In dicotyledons and gymnosperms the stele, which takes the form of a siphonostele, occupies a central position in the stem, and is composed of pericycle, phloem, cambium, xylem, rays, and central pith. The pericycle may be indistinguishable from surrounding tissues or it may take the form of sclerenchyma. Phloem transfers foods and minerals; xylem carries water along the stem; rays are channels through which materials move transversely; the pith seems to have relatively little function.

This type of stele may be continuous, if the rays are very narrow, or dissected if they are wider. In the dissected stele the parts between rays are sometimes called vascular bundles. In either case, the young stem has a cortex and epidermis around the stele.

Monocotyledons characteristically have the scattered type of stele around which there is little or no cortex. The xylem and phloem, with practically no cambium, form into bundles which are scattered about in a rather irregular manner throughout the tissues of the stem. Since there is no functional cambium, growth in diameter takes place chiefly by cell enlargement in most monocotyledons.

All the primary structures of stems develop out of apical meristems, and these, with their wrappings constitute buds. Buds may be dormant, in which case protective scales usually form an outside covering, or they may be active.

Secondary tissues are formed by the action of cambium. Growth in diameter results from the addition of secondary xylem and phloem by cambial action and of cork by the cork cambium. Growth in length results from the activities of the apical meristem and occasionally from meristems at the nodes.

Any solid has three dimensions—length, width, and thickness. Sections cut transversely, radially, and tangentially from a solid block of wood show the different relationships between the various elements of woody tissue. Those cut transversely, cross the tracheids, fibers, and vessels (if they are present) and make longitudinal sections of the ray cells; tangential sections follow the tracheids and other vertically placed elements and cut across the rays; and radial sections follow the vertically placed cells and also the rays which cross them. The various types of lumber owe their peculiarities to a combination of the characteristics of the cells of the wood and the plane in which the wood is cut.

SUPPLEMENTARY READINGS

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See also The Secret of the Southwest Solved by Talkative Tree Rings, *National Geographic Magazine* **56**:737–770.
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Chapter 9

THE PLANT AS A UNIT

A plant does not live in fragments. It is more than an assemblage of individual cells carrying on independent processes. It is an organism composed of coöperating parts, each performing its group of functions. In order to emphasize the significance of these statements this chapter will be devoted to the plant in its entirety.

The following outline should help the student to hold in mind the relationships of the parts of common plants, together with the activities associated with each of these parts.

- Correlations
- Responses
- What is Environment?
- Irritability
  - Tropic Responses
  - Nastic Responses
  - Formative Responses
  - Tactic Responses
- Length of Life
- Structures and Functions of Plant Tissues
  - Conductive Tissues
  - Tissues Concerned with Support
  - Storage Tissues
  - Protective Tissues
  - Glandular or Secretory Tissues
  - Anomalous Structures
  - Vegetative Propagation

If the green shoots of a vigorously growing potato plant which is about to produce tubers are cut off at the ground, some of the underground parts occasionally grow up into the air and develop foliage leaves. Examination of potato plants with young tubers gives a clue to this peculiar behavior, for, besides the roots, rhizomes or underground stems also develop. At the tip of each rhizome an enlargement, gorged with starch and other foods, commonly forms. This is the tuber. The buds and scale leaves are the so-called "eyes" of the potato.

The destruction of the ordinary green, aerial stems of such a plant brings about a revolution in the behavior of the developing rhizomes. Instead of growing horizontally or somewhat downward and forming tubers, their tips now turn upward, extend out into the air, and take the form of ordinary leafy shoots.

From an experiment like this it becomes evident that such a plant acts as a unit and not as a group of independent parts. If this were an isolated example it would be interesting but not very instructive. On the other hand, experiments furnish hundreds of examples more or less similar to this one.

Correlations. The control exerted by one part of a plant over other parts is called *correlation*. The example given above is very striking. A number of others will be cited to illustrate the many ways in which correlations may organize and unify a plant body.

It is generally known that if the terminal bud of almost any plant is destroyed, some of the lateral buds along the sides of the stem lower down, will begin to grow, but if it is left in place, the lateral buds remain dormant. Therefore, the terminal bud, when it is present, in some way retards the rate of metabolism, reduces the frequency of cell division, and prevents the various growth processes in buds at considerable distances down the stem. This action is commonly called *apical dominance*. The explanation of this peculiar behavior lies in the fact that the young leaves and growing apex secrete at least one hormone that travels through the tissues, in some way suppressing the growth of all buds below. With the loss of the end of such a branch the hormone ceases to be produced, and the lateral buds, no longer inhibited, begin to grow. Then they, in turn, bring about the suppression of growth in others that have not yet begun to enlarge.

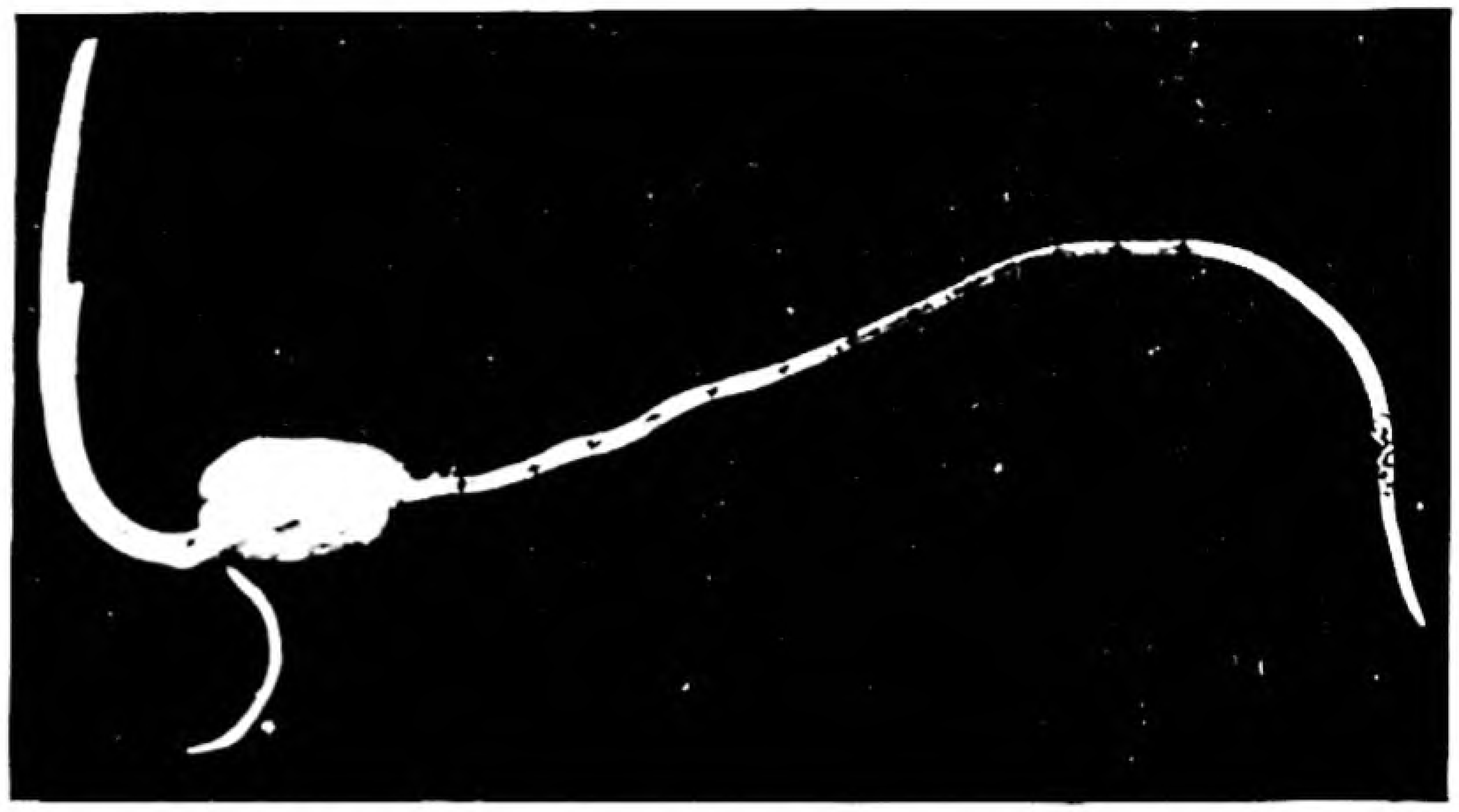
In like manner, the root tips may limit or completely suppress the production and growth of root branches. This action can be readily demonstrated by cutting the outer millimeter or two from the tip of a young, unbranched primary root of a seedling of corn or bean and covering again with moist soil. Within three or four days numerous branches commonly appear as wartlike enlargements over the surface of the treated root. In addition, one or more of these branches is likely to change abruptly from its almost horizontal position and turn downward into an approximately vertical direction.

An even more striking evidence of the controlling effect of growing tips is to be seen in trees with excurrent branching such as the firs and spruces. If the "leader" or upper part of the main vertical shaft of such a tree is destroyed near the terminal bud, one or two of the lateral buds or young shoots just behind the wound may begin rapid growth, turning upward, assuming the lead, and keeping the form of the tree much as it would have been without the loss of the leader. If the leader had been allowed to develop normally, this lateral branch would have grown outward instead of upward. In both of these cases the apical regions influence not only the amount of elongation but even the direction in which the branches grow.

Two other examples taken from the experience of florists will further emphasize the importance of correlations in plant organization. It has long been known that in propagating many kinds of plants by means of cuttings, roots are much more certain to be formed if there is present on the cutting at

Dead leader of Douglas fir tree being replaced by one of the lateral branches.

least one actively growing bud and a few young leaves, than if the shoot has none but dormant buds. It is now known that the growth substances that form in active buds are responsible for the growth of roots. And, finally, almost every flower fancier has observed the fact that allowing seeds to mature on blooming plants frequently reduces the size and numbers of flowers or may even entirely halt their formation. For this reason the flowers are commonly removed before the petals fall from such plants as sweet peas, nasturtiums, and pansies, in order to cause these plants to continue to bloom.



Responses of roots. Corn seedling turned on side for a few hours. Roots responding by changing direction of growth. Ink marks originally equidistant throughout length of root. Bending occurred at region of elongation.

In these and hundreds of other situations, there is ample proof that active protoplasm throughout the plant is continually responding to its environment in a multitude of ways and that the various parts act together in a more or less well unified and correlated manner.

Responses. A *stimulus* is any condition or environmental factor that brings about activity on the part of protoplasm, and the resulting action is the *response*. The correlations described above are responses of one portion of the plant to the internal environment produced by the functioning of other organs. But a very great part of its environment lies entirely outside the plant.

If a flower pot in which a young bean seedling is growing is inverted, much twisting and bending of almost every part of the plant ensues with concomitant important though invisible altered activities within the tissues. If the seedling is three or four inches tall and growing rapidly the most obvious movements begin to take place within an hour or two. Leaves begin to change position by a series of distortions of various parts and the entire shoot soon bends back on itself, forming a U, even growing up against the soil above it.

Although these activities in the shoot are out in the air and light where they are easily seen, the roots in the soil usually bend quite as much as the leafy shoot. Not infrequently they even emerge from the soil and grow out into the air where they eventually die from lack of water.

What has been said concerning a bean seedling is equally true, with minor variations, of almost any young plant or actively elongating parts of older ones. In each of these instances the mere change of the direction in which gravity impinges on the growing tips of roots and shoots has set up chains of reactions which, together, have greatly altered both the form of the plant and the functioning of its parts.

Under the influence of the numerous environmental forces, active protoplasm reacts in many ways. It may build thicker or thinner cell walls; it may produce larger or smaller cells; it may secrete certain enzymes, hormones, or other substances, or it may fail to secrete them; and it may grow more rapidly in certain places than in others, thus changing the shape of various organs of the plant. In fact, the countless variations in plant form, structure, and activity result from the adjustments of the protoplasm to the myriad combinations of environmental factors.

The structure and types of responses of the protoplasm of the various plants are under the control of heredity. That is to say, the combinations of genes in each plant cause its protoplasm to be sensitive to certain sets of stimuli. Hence each individual reacts in its own peculiar way. Thus, if a mushroom and a fern are growing side by side in a

forest, the protoplasm of the fern will secrete chlorophyll under the stimulus of light. The fungus, on the other hand, will remain entirely devoid of chlorophyll because its cells are entirely incapable of producing it.

What Is Environment? Thus far the word, environment, has been used occasionally, being defined as the surroundings of an organism. Sometimes, by a figure of speech, the word is almost personified, as when terms such as "the directive action of environment" are used. Expressions denoting purpose or planning should be avoided entirely or used with greatest caution, for purpose and planning cannot properly be attributed to factors such as heat, light, temperature, water, gravity, soil, and neighboring plants and animals. Neither should we think of a plant as "seeking" light or water, "trying to find" mineral nutrients in the soil, or "reaching out for" some other necessity. These expressions usually connote volitional power commonly ascribed to human beings, and apparently plants are totally lacking in such mental attributes. Instead, they respond in what seems to be a most mechanical manner without plan or purpose. It is true that, under usual conditions, a vast majority of their reactions tend to perpetuate their lives, but some responses seem to be only incidental or without value. Obvious examples are the scattered hairs on leaves or blotches of color on stems which some plants develop when growing in very strong sunshine or in extremely dry locations. Just as some people, when exposed to sun and wind become freckled, so plants react at times in a way that seems to have little or no meaning. The explanation would seem to be in both cases that a chance gene complex, acted upon by some phase of environment, happens to produce the insignificant result observed.

Both the environment and responsiveness to it are extremely complicated. To add to the complexity of this situation, the plant often responds at the same time to two or more factors in its environment, and these reactions may work together to the same end or they may be somewhat antagonistic. To understand the behavior of a plant, therefore, a single factor at a time should be studied in order to sort out the elements of its reactions.

Irritability. Responsiveness of protoplasm to environmental stimuli is often called *irritability.* Responses appear to be of several types, and the underlying causes of these reactions are understood only in part. In a general way they may be classified as *tropic*, *nastic*, *formative*, and *tactic*.

TROPIC RESPONSES. This type is one in which a part of the plant, as for instance a stem, a leaf, a root, a flower, or a fruit turns or bends (*tropos*, turning) from its usual direction of growth into another position that is definitely related to the direction from which the stimulus comes. That is to say, the reacting organ turns toward the source of stimulus, away from it, or at some other rather definite angle in reference to it, as when stems and leaves of house plants so bend as to face the nearest window.

Any such reaction is named by combining a descriptive prefix to the word *tropism*. Thus we have *geotropism*, response to gravity (*geo*, earth); *phototropism*, response to light (*photos*, light); *chemotropism*, response to a chemical element or compound, such as oxygen, carbon dioxide, or nitrate; and *thigmototropism*, response to touch (*thigma*, touch). The last can be illustrated by tendrils, which respond by wrapping themselves around the objects with which they come in contact.

Tendrils. (A) Garden pea. (B) Virginia creeper. (C) Whole leaf of *Clematis* acting as a tendril.

If a plant organ reacts by turning toward the source of a stimulus, it exhibits a *positive* tropism; if away, the response is *negative*. Thus many roots grow downward under the influence of gravity, affording an example of a positive geotropic re-

sponse. Shoots, on the contrary, usually grow upward, partly because they are negatively geotropic. Plant organs also may respond to numerous other stimuli in a positive or negative manner.

Plants differ greatly in both the type and strength of the reactions of their parts. The types of responses of each kind of plant appear to be inherited. For this reason, every species tends to develop its own specific shape by reacting to sets of environmental stimuli. In other words, plant form varies with the combined effects of heredity and environment. If properly interpreted, this fact largely explains the tall spire of the Lombardy poplar, the conical shape of the fir tree, the round top of the apple tree or cottonwood, the twining vine, or the creeping purslane, and the multitude of other plant forms.

Gravity, light, and moisture are the external stimuli that most profoundly affect the majority of plants. A study in detail of each of these will help more fully to interpret many factors of their behavior. To test the effects of each stimulus it is necessary to remove or modify it without otherwise changing the general environment of the plant. It is much easier to do this with moisture and light than with gravity.

GRAVITY. Since it is impossible to take a plant to a place where there is no gravity, some substitute must be used, or the plant may be placed in such a position that gravity acts upon it from an unusual direction.

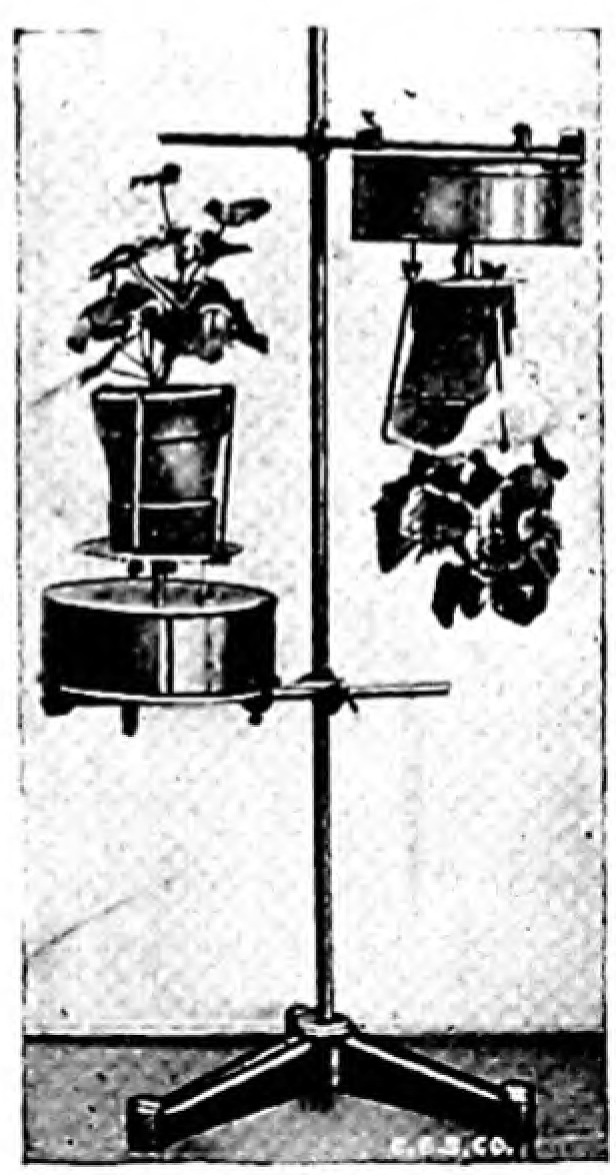
The last of these methods is the most easily followed. A potted plant is simply laid on its side or turned upside down and allowed to grow in the dark, so that light is eliminated as a stimulus. In a short time the shoot grows up and the roots bend down.

An experiment first reported in 1805 by the English botanist, John Andrew Knight, substitutes centrifugal force, the force which causes objects to fly off of a rapidly rotating body, for gravity. Germinating seeds are securely attached to a disk in such a way that they can be supplied with sufficient moisture, and rotated rapidly for several hours around a horizontal axis. Because of the swiftly changing position of the seedlings, gravity can have no continuous effect upon them, but centrifugal force pulls on each one in a direction away from the center of the disk and toward the outside. Although the primary roots are pointed in various directions at the beginning of the experiment, they are found, at the end, to have bent into such positions that all grow toward the periphery, which reaction is the same as growing *down* in response to gravity. If suitable seedlings have been used, such as those of corn or peas, the young shoots turn toward the center of the disk.

In an experiment developed by the German botanist, Pfeffer, the plant is placed on a rotating disk in the dark and caused to turn slowly around a horizontal axis. The continual change in the position with respect to gravity gives the plant no opportunity to respond to that stimulus, and it usually grows straight forward.

The most definite negative geotropic response of the shoot often exhibits itself at the time of germination. Whatever the position of the seed in the soil, the shoot finds its way upward. How is it possible to be sure that this is not a response to light? Is this reaction of any obvious value to the plant?

LIGHT. In many respects the reactions of plants, especially of their stems, to light are exactly the



Pfeffer's clinostat. The mechanism can be adjusted to turn the specimens slowly on a horizontal axis, causing them to be stimulated on their various sides by gravity. (Courtesy, Cambosco Scientific Co.)

Geraniums responding to light. (*Left*) Plant lighted from above in greenhouse. (*Right*) The same plant receiving light from side through a window.

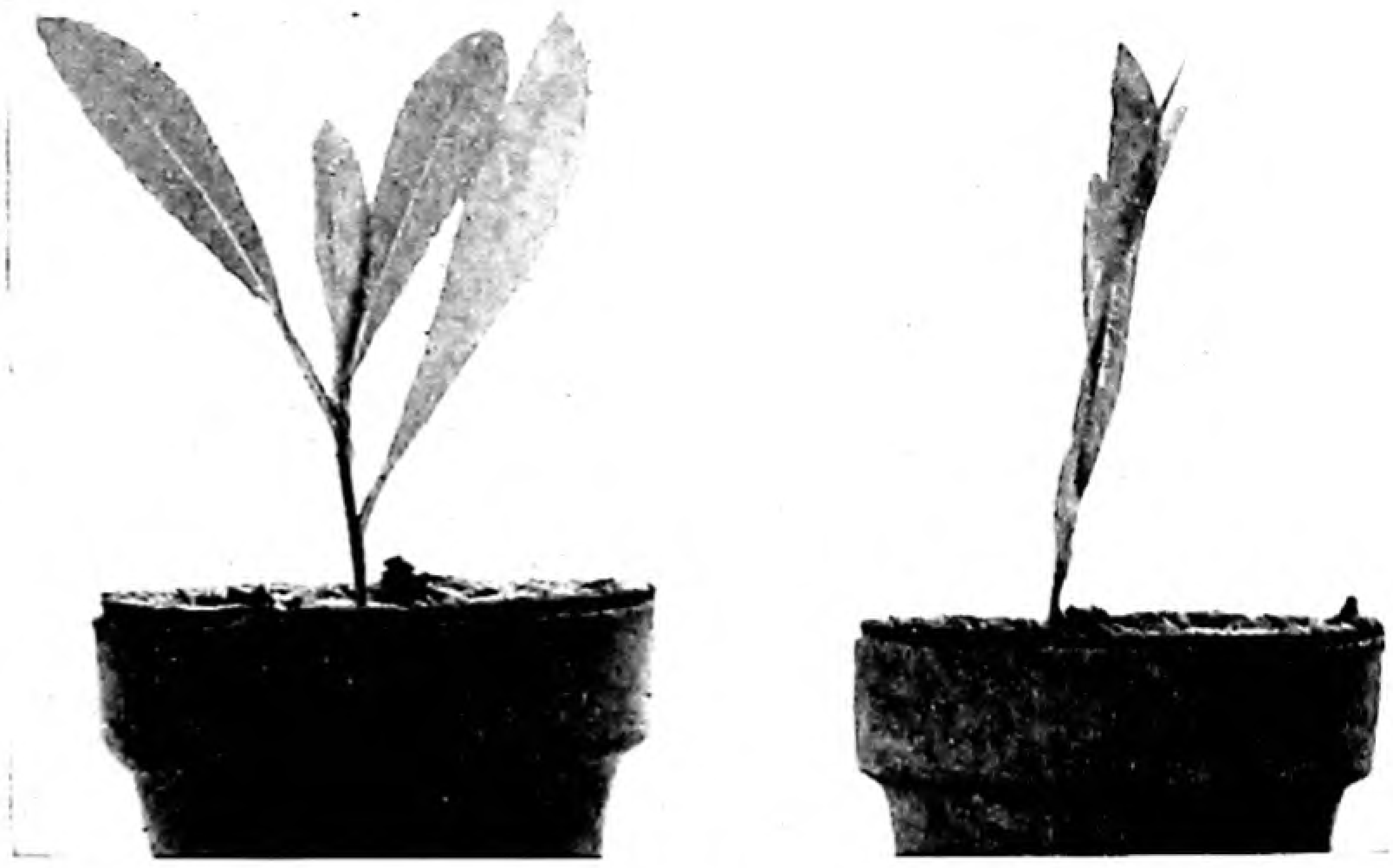
reverse of those to gravity. But since light and gravity usually act from opposite directions, the responses of the plant to the two actually coöperate in producing similar directions of growth. Thus, a shoot reacting positively to light and negatively to gravity, tends to grow upward because of both stimuli. But if the source of light is not from above, the shoots and leaves usually turn toward the light, or in many cases they face somewhat above it because of the effects of gravity. This combination of effects explains the position assumed by house plants when they grow toward, but not directly at, the nearest window.

When growing in strong sunshine the leaves of certain plants twist on their axes until the blades face east and west with the edges assuming a north-and-south position so that the noonday sun strikes the edges of the leaves. One of the best known and most widely distributed of these *compass plants* is the wild prickly lettuce. The meaning of this action, if it has meaning, is unknown.

There are a few well-known plants whose young stems have a negative response to strong light. One of these is the Virginia creeper. Shoots of this plant grow directly toward shade and may even grow into places under overhanging cliffs or under porches so dark as to prevent the development of chlorophyll. Such starved shoots may even die without showing a positive reaction to the weak light that reaches them. Doubtless a negative response to light may often cause this plant to come into contact with suitable surfaces on which to climb, such as stone walls or tree trunks, because of the shadows which they cast. This type of behavior is usually, but not always, advantageous to the plant.

MOISTURE. Many roots have a distinct positive hydrotropic response. For this reason those of willows and cottonwoods often clog tile drains, turn-

ing away from their normal directions of growth and crowding into the greater supplies of water immediately around and within the tiles. In contrast with these, roots of many kinds of plants respond negatively to liquid water or mud, remaining in moist soil. The entire root systems of some swamp and peat bog plants develop just above the water level. They are therefore limited to the upper three or four inches of soil. This reaction, however, may not be a negative response to water as it appears to be, but rather a positive one to oxygen.

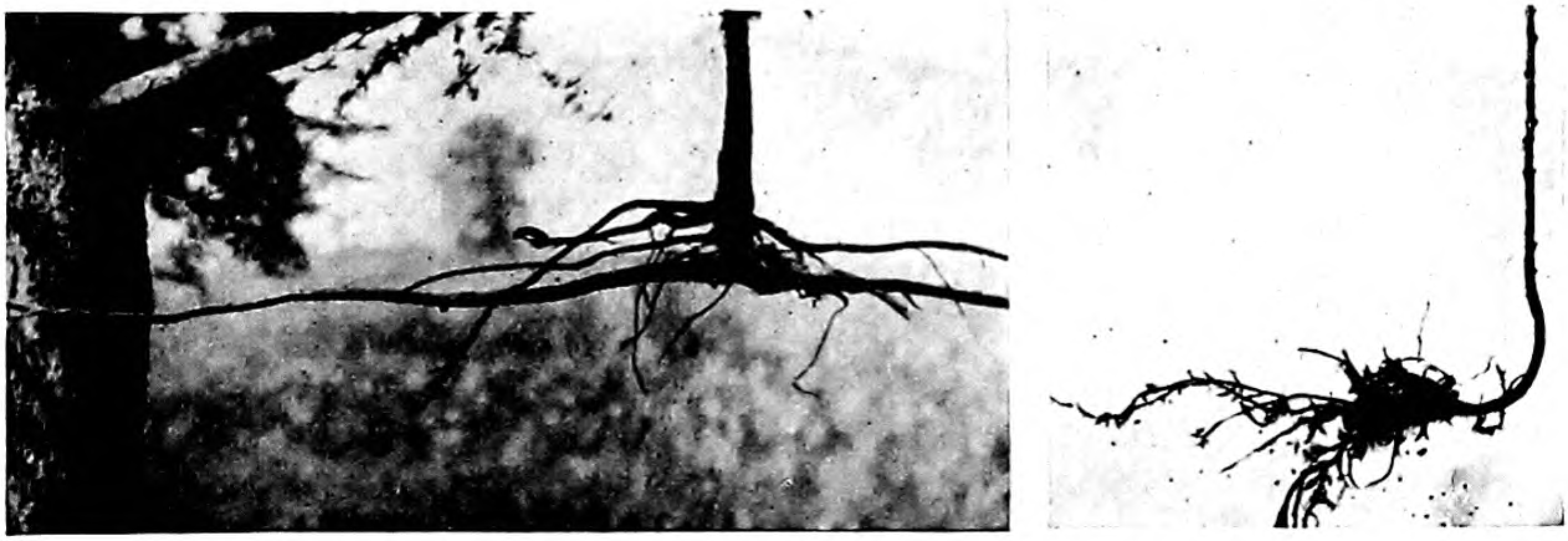


Prickly lettuce acting as compass plant. In picture at left, camera faced toward the west; in the one at right, toward the north.

Positive hydrotropic responses of roots should not be interpreted to mean that they sense water at some distance and go in search of it, but rather that if the soil against one side has more moisture than has that against the opposite, the root grows toward the moist side, thus entering the soil that contains the greater amounts of water.

Water not only affects the direction in which the roots grow but also the amount of growth. Common land plants usually have the best root development in soil that is moderately moist, therefore having fairly balanced water and oxygen supplies. In either very wet or very dry soil they develop less extensively. What are the probable reasons?

THE MECHANICS OF TROPIC RESPONSES. In the tropisms of common plants all changes in form take place only in the younger growing parts. Old leaves and the older stems and roots remain unchanged in position. The regions of growth can be exactly determined by placing marks at equal distances on the various parts and then allowing them to grow for some time. A change in the spacing of the marks will, of course, show just where growth takes place. If a plant is marked and then caused to bend in response to some stimulus, the bend occurs at exactly the place of elongation, while other parts that do not grow, hold their original shapes. This fact shows that tropisms are brought about by differential growth rates. Thus, when a plant is bending toward a lighted window, the lighted side does not grow as rapidly as the shaded side.



Horizontal roots of young larch trees, growing just above water level in peat bog.

It can be shown that the portion of the plant organ which bends is sometimes a short distance away from that which receives the stimulus. For example, if the upper millimeter or two at the tip of a millet or oat seedling that has grown in the dark, is removed, or if it is covered with a lightproof cap, no response to light occurs. If, however, the tip is exposed to light for even a brief period, the bending of the shoot occurs perhaps a centimeter lower.

Since the region of perception is in the upper millimeter of the shoot, and the region of response is some distance below, there must be a transfer of the stimulus. There have been a multitude of attempts to explain this phenomenon. It would seem at first glance that the plant had something like nerves, but numerous investigators are now accumulating a mass of evidence which shows that these differences of growth rates are controlled by *growth substances* (see p. 43).

A few of the experiments by which these facts have been determined should be instructive here. If the tip of a shoot of an oat seedling that has been growing in the dark is cut off, exposed to light for a time, and then replaced, or attached to another cut shoot, growth is resumed. If, instead of placing

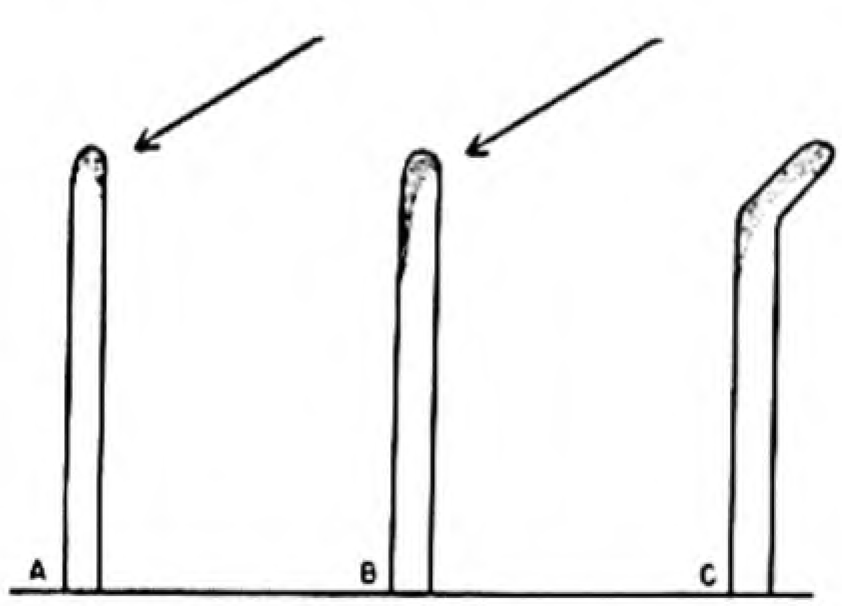


Diagram illustrating action of auxins. Shaded parts indicate portions especially well supplied. (A) Apical region being stimulated by light and beginning to produce growth substance. (B) Migration of auxin along shaded side. (C) Bending in region of elongation caused by rapid growth brought about by growth substance.

the tip on the center of the cut stump, it is attached at one edge, there is more rapid growth in the tissues directly under the contact and a consequent bending of the shoot because of differential elongations. But, it may be argued, is not this a result of direct stimulation of cells through the contact of the cut surfaces? To answer this question, tiny blocks of gelatin may be inserted between the two. Under these conditions growth takes place as soon as the hormones have had time to diffuse through the gelatin.

To guard this experiment more completely against error, blocks of gelatin may be placed in contact with the cut surfaces of tips of shoots growing in the light, left there for a time, and then placed on the cut ends of shoots which have been kept in the dark but in which growth has stopped because of the removal of the tip. Under these conditions growth is resumed, strongly indicating that a growth-promoting substance has entered the gelatin from the stimulated tip and then diffused out into the inactive stump.

The question remains, however, as to how this mechanism can bring about the bending of a shoot toward the light in onesided illumination. Additional experiments have shown that while light stimulates certain cell masses in the stem tip to secrete growth substances, it also makes protoplasm less permeable to them, thus reducing the amount that can diffuse into the cells of the illuminated side of the stem, consequently slowing its growth rate. This effect seems to be strengthened by the fact that light also makes the tissues it strikes less sensitive to the auxins they may contain. The tissues on the shaded side, then, are stimulated to grow more rapidly both by the larger amounts of hormones reaching them and by their greater sensitiveness to them, thus bending the stem toward the light.

Responses to gravity also appear to be brought about by migrations of auxins. When a plant is placed in a horizontal position hormones move to the lower side of both stems and roots. The stem, therefore, grows more rapidly on the lower side, causing it to bend upward. The fact that the root bends downward is explained in another way. Auxins in the tissues of a root, unless very dilute, retard growth. Therefore, when the lower side of a horizontal root is restrained from elongating, the more rapid lengthening of the upper side causes it to bend downward. Thus, while one part of the

mystery of tropic responses seems to be nearing solution there remain other unsolved problems. At present, information is lacking as to why the tissues of the root and shoots of the same plant react to growth substances in very different ways. It is clear, however, that auxin is produced in the apical region of the shoot under the influence of the short (blue) wavelength of light. It is derived from tryptophane, one of the amino acids. Once formed, it can migrate toward the lower parts of the plant through living cells at the rate of about one centimeter per hour. It does not reverse its direction, neither does it turn aside into lateral buds or shoots. They produce their own auxin. Under the influence of certain oxidases auxin is destroyed, thus reducing the growth in the cells where this action takes place.

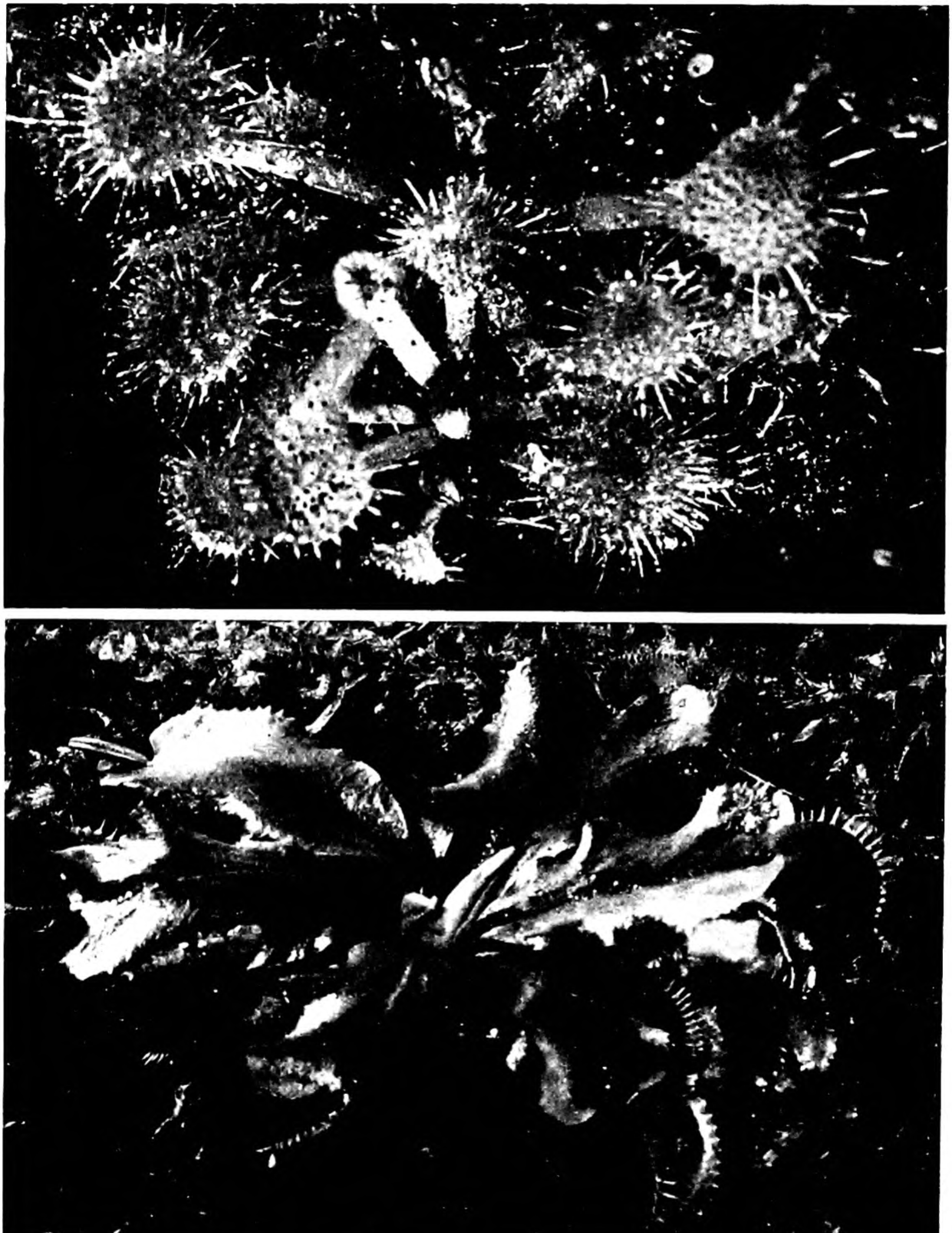
When the presence of growth-promoting substances was first discovered, plant physiologists immediately began investigations to find out what these substances really are. Recently three pure auxins have been isolated from plants, all appearing to be much alike in their effects upon growth, and some dozens of other compounds, not known to occur in plants, have been found to give similar results (see p. 51). Some of these will cause bending if a solution is applied on the side of a growing portion of a stem. In other instances, the development of adventitious roots on the sides of stems is promoted, and petioles can be made to grow upward or downward by applying the solution in the proper place.

When auxin is present in a suitable very dilute concentration, meristematic activity is promoted. Apical and cambial growth as well as the growth of other immature cells is stimulated. Mitotic division takes place, increasing the number of cells; but any considerable added amount brings mitosis to a halt. The reason is not clear. It seems that the correct concentration develops in woody plants in the spring, for both apical meristems and cambium become active at the same time. Likewise, these meristems cease to grow during the latter part of the summer. Growth in size of cells is controlled by auxin in a different manner. The primary walls of young cells are known to be made extensible under the influence of growth substance; therefore they offer little resistance to turgor pressure within the cells. Usually the cellulose fibrils are so oriented that the walls can elongate more than they can extend transversely. For these reasons young cells grow in length especially. When secondary walls are added, the structure becomes too firm to permit further extension, and enlargement comes gradually to an end. It seems probable that these combined facts help to explain the development of growth rings in trees as well as the annual increase in height.

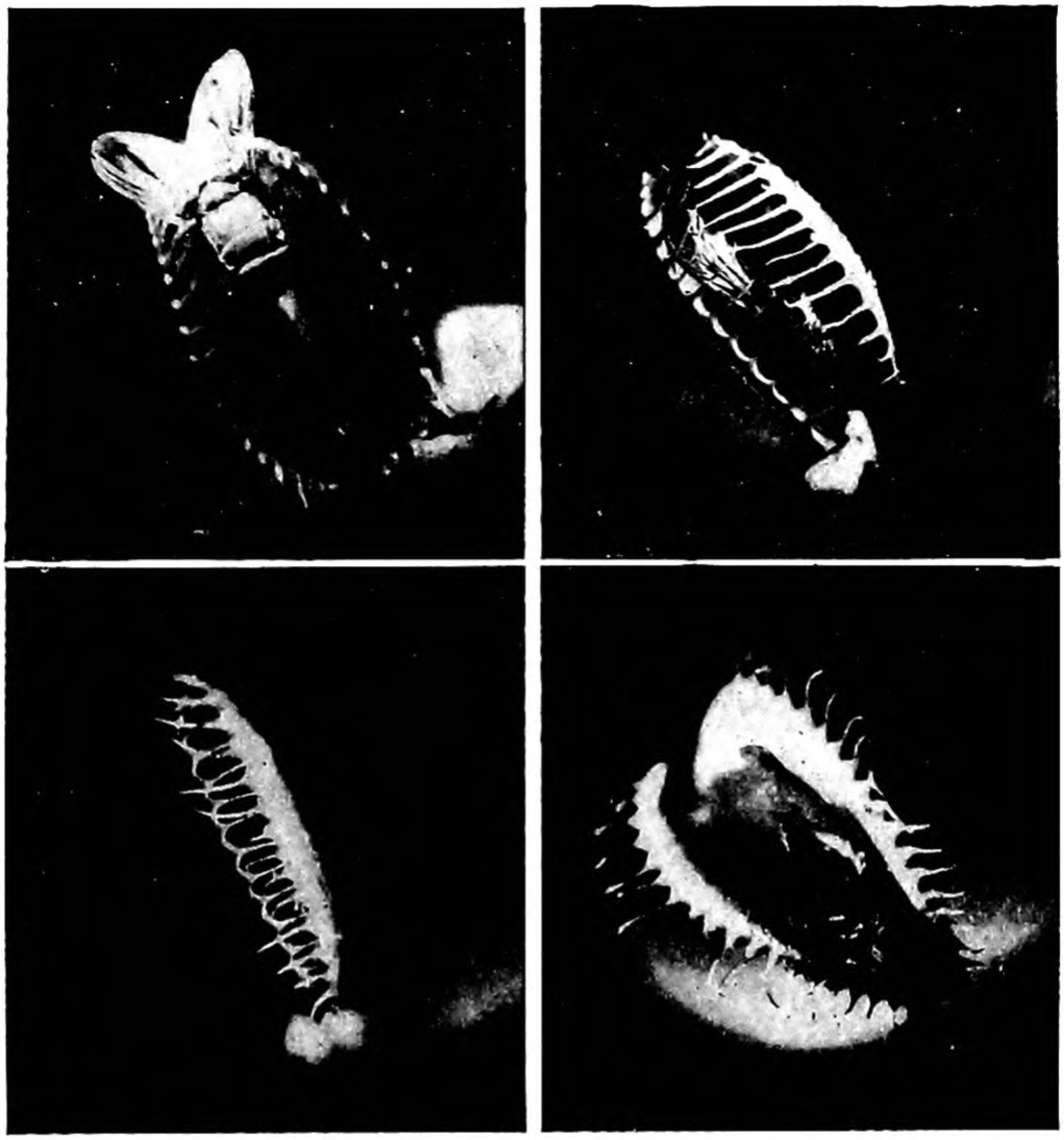
For many years some botanists were inclined to believe that, when a proper technique could be devised to demonstrate it, a type of nerve structure would be found to account for the various adjustments and responses which occur in plants. While the action of plant hormones does not prove the absence of nerve impulses, so many of the unifying actions that appear, superficially, to be controlled by nerves are known to be brought about by auxins, that it seems probable that these growth substances provide the answer to the entire problem.

The tropic responses described above are all brought about by different amounts of growth on opposite sides of the responsing structure. They are, therefore, called *growth movements*. In these, changes in position take place relatively slowly. The more rapid type described below is also a bending action and therefore a tropic response. The motions involved here are brought about by changes in the amount of pressure within the cells. For this reason they are called *turgor* movements. As examples, a light touch to the stamens of the flowers of some of the cacti causes them to move quickly and to bunch themselves about the place that was stimulated. Likewise, touching the base of the stamen of barberry with the tip of a needle, or even the end of a stiff bristle, causes it to react in such a way that the anther slaps the stigma. These movements of floral parts doubtless aid in pollination through the agency of insects, but their actual value to the plant is debatable.

The remarkable responses made by some insectivorous plants deserve brief mention here. In Venus' flytrap the blade of each leaf is in the form of two lobes hinged together with a joint which



Insectivorous plant. (*Top*) Sundew, showing sensitive hairs. (*Bottom*) Venus' flytrap. (Courtesy, General Biological Supply House.)

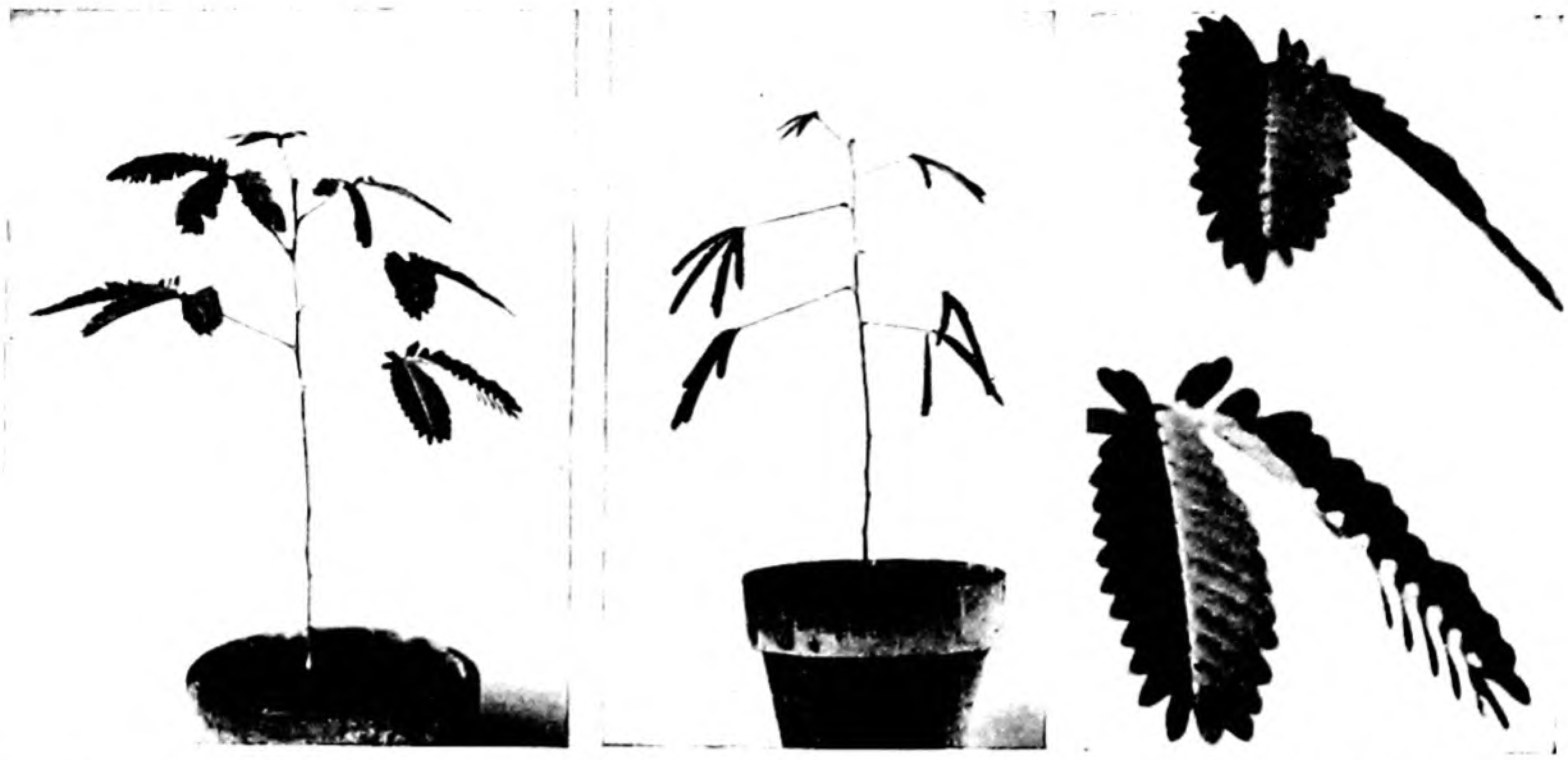


Response in Venus' flytrap, an insectivorius plant. Photos show four steps in the ensnarement of a fly by a leaf of the plant. (Courtesy, General Biological Supply House.)

can open or close somewhat like a book. When a small insect alights on either of the lobes, or some other object stimulates them, the two close like a trap and often hold and digest the victim. The sundews, on the other hand, have leaves covered with long hairs, each bearing a rounded gland at its outer end. These glands produce a sticky secretion in which insects sometimes become entangled. Then the surrounding hairs bend toward the victim in such a manner that a number of their tips are brought into contact with it. These reactions are followed by the digestion of the insect and the absorption of food from it, much as in the Venus' flytrap.

These various motions of plant parts take place because, under the influence of the stimulus, cell sap rushes from certain turgid cells either into other cells or into neighboring intercellular spaces. Such changes of pressure bring about the rapid curvatures described.

Nastic Responses. This type contrasts with tropic responses in that the nastic response is not controlled by the direction of the stimulus. As examples, the leaves of clover, oxalis, castor bean, locust, acacia, peanut, and many other plants assume a "sleep" position at night, that is, the leaves fold in response to a lower temperature and darkness. A similar behavior is shown by many flowers such as those of dandelions and tulips, which close at night, while still others, such as evening prim-



Sensitive plant. (*Left*) Undisturbed. (*Center*) A few seconds after the leaves were touched. (*Right*) Enlargement showing pulvini as light spots at bases of leaflets.

roses, morning-glories, and some kinds of cacti open at dusk or after dark and usually close in the morning.

The leaves of many members of the clover family fold when they are stroked. One of the most striking responses of this type is displayed by the sensitive plant, *Mimosa*, a native of tropical America, which is easily grown from seed in any laboratory where ordinary tender plants can be cared for. A light touch or a slight breeze will cause the leaves to fold quickly. Plants such as this have a special organ, the *pulvinus*, which is the agent of motion. This can be seen as a swollen structure at the place of attachment of each leaf or leaflet. It is so constructed that the permeability of the protoplasm of certain of its cells changes when the plant is stimulated, allowing water to pass out into the intercellular spaces, thus reducing the turgor of the cells. In other words, a situation very much like wilting comes about in the supporting tissues of the pulvinus, with the consequent drooping or folding of the parts concerned. Within a few minutes after these motions have been carried out, the cells of the pulvinus again become turgid and the leaves assume the normal position. The manner in which these rapid changes in permeability and consequent turgor are effected is very poorly understood.

FORMATIVE RESPONSES. Formative responses are those in which the activities or products of the cells are influenced or altered. As an example, water and oxygen, when applied to most kinds of seeds at the proper temperature, induce certain of the cells to secrete many kinds of enzymes which are very active in germination and growth. Some of these secretions bring about the digestion of the various kinds of foods and others have respiratory functions. Just how many of these enzymes are produced under these conditions no one knows, but without some of them, seeds could not germinate.

Other formative responses are those in which the permeability of the plasma membranes of cells is changed as a result of the actions of certain chemical compounds. As an example, if some nutrient solution, such as potassium nitrate or potassium chloride, is applied to cells, their membranes become more permeable, permitting substances, which would otherwise be unable to diffuse through them, to enter or leave. Compounds such as calcium nitrate, on the contrary, make protoplasm less permeable. Therefore, changes in the minerals around roots may partly control the kinds of material that enter or leave the plant, as well as the amount and rate of movement of these materials. As a secondary consequence of these changes

in permeability, the turgor pressure within the cells may vary. How could these changes in turgor occur?

One set of formative responses has dryness or excessive transpiration as its stimulus. The exact kinds of adjustment to drying conditions differ greatly in various plants, but some of the most effective are in the form of thickened walls of the cells that are exposed to dry air. Thus, the epidermis of a large number of plants produces much thicker walls when growth occurs under conditions of high transpiration than when it occurs in moist air. Besides the production of thick epidermal walls, some plants secrete additional coats of cuticle and waxes which spread over the surface of the epidermis, creating a waterproofing that is more or less complete.

TACTIC RESPONSES. These occur in free-swimming organisms and in certain specialized swimming cells of complex plants which travel toward or away from some stimulus (*taxis*, arrangement). This type of response may be illustrated by certain unicellular green plants which will congregate in the illuminated side of a jar in which they are living. Others react to weak solutions of chemicals such as sugars, acids, or oxygen. In this respect these plant cells behave very much like primitive animals.

Tactic responses are named by prefixing the name of the stimulus to the root word, *taxy*, as *chemotaxy*, a response to a chemical, or *phototaxy*, a response to light. Since these reactions occur only in microscopic forms, they are not important at this point but will be so in the study of more primitive plants in later chapters.

Length of Life. Some plants, such as corn, beans, and cotton, live during only one growing season. These are *annuals*. In some species of annual plants the seeds germinate in the autumn, and growth continues intermittently during the winter, the plant flowering and producing seeds the next spring or summer and then dying. A plant of this kind is a *winter annual*. Good examples of this type are winter wheat and turnips planted in the fall in climates in which they do not winter-kill. A considerable number of native species that succeed in arid regions are winter annuals which complete their life cycles during the time of winter rains, thus enduring the dry summer as seeds.

Biennials require two growing seasons in which to reach maturity. During the first year of growth they store food in considerable amounts, and in the second they produce flowers and seeds, after which the plant dies. Many of the weedy *rosette plants* such as evening primroses, mullein, thistles, and shepherd's purse are biennials, as are also such garden vegetables as beets and parsnips. In all these plants the main upright stem does not grow appreciably in length during the first year. Its leaves remain crowded close together near the ground, forming

Rosette-forming biennial weeds. (*Top*) Thistle. (*Top, left*) Year-old rosette. (*Top, right*) Two-year-old plant in bloom. (*Bottom*) One-year-old rosettes of a wild mustard.

The beet, a biennial food plant. (*Left*) Enlarging root during first summer. (*Right*) Utilization of reserves in production of seeds in two-year-old plant.

an almost circular leafy tuft, the rosette. In garden practice, biennials are harvested at the end of the first growing season, at the time when the maximum amount of food is present. For this reason one seldom sees vegetable biennials in flower. If left to complete their life cycle they would use their entire supplies of reserve foods in growing tall stems and in the production of flowers and seeds and therefore would be without value as human food. Other rosette plants such as dandelion and plantain keep this form indefinitely, living for many years.

The biennial type of rosette is especially common in grasslands that have been plowed or otherwise disturbed, while plants that keep the rosette form throughout their entire lives are to be found in great numbers in arid and semiarid climates and above timber line on high mountains.

In places like these where vegetation is low and therefore rosettes on the ground receive ample light, this type of leaf arrangement doubtless is of advantage to the plant. The leaves are so placed that they do not shade each other to a very great extent, while at the same time they are protected from winds by lying flat against the ground; humidity is greater there than at higher levels, thus reducing the drying action of the air; in many places, especially in mountains, snow may add its protective cover to the entire plant during the most severe part of the year. When seeds are produced, they almost always develop on some sort of stalk from which they are more readily scattered than if they ripened at the surface of the ground as may be seen in the illustration.

Perennials are plants which live indefinitely, or at least through more than two years. Trees, shrubs, certain garden flowers, many weeds, and most of the wild grasses are good examples. Some of these live over a period of only a few years. The "century plants" grow vegetatively for many years—not as much as a century, however—then flower and die; and the "big trees" of California or the cypress trees of Mexico may live for thousands of years.

Structures and Functions of Plant Tissues. Despite a considerable diversity of structure, the stems, roots and leaves of all higher plants are fundamentally alike in organization and to some extent in functions. All have epidermis on the outside, at least for a time, and all have steles constructed, in part, of xylem and phloem. Stems and roots of gymnosperms and dicotyledons develop cambium as a part of the stele, although in herbaceous plants the cambium may remain inactive or produce only a few xylem and phloem elements. Roots and stems of monocotyledons and ferns do not have a cambium except in rare instances. Cambium may form in the midribs of dicotyledon leaves but does not become active. The cortex lies between the epidermis and the stele. It is always easily recognized in the roots and in some stems, but in many stems, especially those with scattered steles, there is not a sharp dividing line between it and the stele. In leaves it is specialized to form the mesophyll.

The great general functions of plant parts, aside from the rather localized activities of absorption and synthesis, are conduction, support, storage, protection, and secretion. These may be summarized in the order named.

Conductive Tissues. After water is absorbed into the roots, most of it enters the vessels or tracheids of the *xylem*. These are perforated with numerous pits, or thin places in the walls, permitting water to pass from one to another. This construction allows the root, stem, and leaf to contain a column of water which extends from the root tip to the ultimate veinlets of the leaves and which is divided among the multitude of tubes.

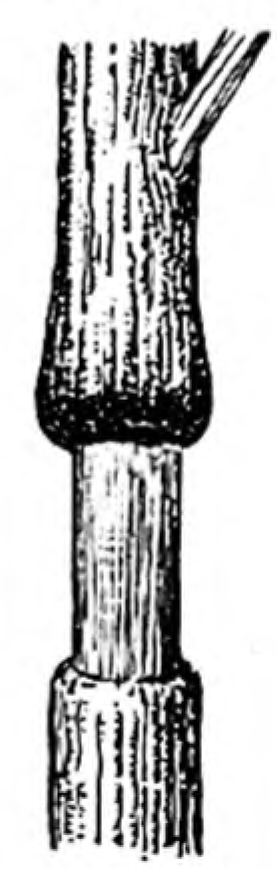
In a similar way the *phloem* forms a continuous channel through which sugars and proteins travel from the leaves to the stems and roots. It is as yet impossible to determine just how substances move in the phloem or even to be certain which kinds of the phloem cells are active in carrying these materials, but it is evident that such transfer takes place. It should be understood that the phloem lies parallel with the xylem throughout the length of the plant.

The *rays* also are a part of the conductive system. They transfer water from the xylem across the stem or root to any cells that may be somewhat distant from the sources of supply. In the same way foods are probably carried from the phloem to various living cells which would otherwise be out of reach of food.

Translocation of Materials. Water and the minerals dissolved in it, which enter the plant at the tips of the roots, may eventually find their way to the leaves or other distant parts. In a tall tree water must travel hundreds of feet from root tip to leaf. On the other hand, the parts of a plant which are not green must have food and growth substances from the leaves and stem tips, and all the cells everywhere usually require oxygen. The fact that it is necessary for materials to travel in both directions, sometimes the full length of the plant, in order that life may continue, raises the question of the channels through which such transfers take place and how the substances move.

Numerous methods have been employed to determine just where and how transfer takes place in a plant. Some of these methods that are still in use, both in general laboratory work and in research, were devised centuries ago by pioneer investigators.

Early Experiments. More than 250 years ago, an Italian scientist, Malpighi, in attempting to discover the channel through which water travels in plants, removed narrow rings of bark from twigs. He found that the leaves on portions of the stem above the rings of destroyed bark did not wilt.



Twig with a zone of bark removed down to the xylem, showing enlargement above caused by accumulated food that could not continue to migrate downward because of destruction of phloem.

He also noticed that the parts below the rings did not continue to grow in diameter, but that the stem enlarged rapidly just above the cut. From these observations he concluded that water travels through the wood and that foods travel through the bark. Do these conclusions from the experiment seem valid?

Other investigators made another approach to the problem. A slit was made in the bark large enough to permit the removal of a short section of the wood across the entire diameter of a stem, thus destroying all connections between the wood above and below the cut while leaving intact the greater part of the bark. In this experiment the leaves wilted promptly, and the part of the plant above the destroyed wood soon died. Do these results support Malpighi's conclusions? In the light of your knowledge of stem structure, just what tissues were destroyed in each of these experiments?

Both of these investigations have been repeated many times, and both have been somewhat refined. Results all agree, nevertheless, in showing that water travels from the roots to the leaves through the wood of the plant and that food moves from the leaves through the bark. But both the wood and the bark are composed of many kinds of cells. Therefore, this general statement as to the pathways through which substances travel must be made more definite.

The Water-conducting Tissues. Research workers of the present day agree fairly well that water rises, for the most part, through the tracheids and vessels of the xylem. A slow migration doubtless occurs through the walls of these xylem elements, and there have been those who believe that the walls rather than the openings of the cells are the channels through which such conduction takes place. Nevertheless, it is difficult to understand how such slow movement of water molecules could account for the relatively rapid rise of water in stems. Water may move upward some inches per hour in rapidly transpiring shoots, but in the process of imbibition in a block of dry wood it requires days to travel equal distances.

A simple experiment easily demonstrates the fact that the water may rise as a liquid through the cavities of the vessels and tracheids of the xylem, although it cannot be said to prove that it travels in the same way in a plant growing normally with its roots in the soil. The cut end of a leafy twig or of a root of a plant that is transpiring rapidly, is placed in a solution of a suitable dye for from 30 minutes to a few hours. Sections of the stem are then cut at different levels to determine the tissues through which the dye has risen. The colored parts are found to be limited always to the water tubes and tracheids of the xylem. Although this experiment seems to answer the question, it must be recognized that the cutting of the stem and the consequent severing of the xylem elements introduces an unnatural factor into the experiment. Since there is at present no fully reliable method of proving or disproving the point, the majority of botanists await a fully convincing proof, realizing in the meantime that the evidence strongly points toward the vessels and tracheids of the xylem as the main channels of water transportation.

How Water Rises to the Tops of Tall Trees. Although it is possible to be reasonably certain of the channels by which water is conducted through root, stem, and leaf, the problem of the mechanism by which it moves in the plant still remains. This is an old question and although numerous attempts have been made to answer it none of the explanations has been fully accepted by all botanists. Within comparatively recent years, however, investigation has resulted in a hypothesis which is standing the test in the hands of the majority of workers. This explanation is sometimes challenged, but it seems more nearly to explain the observed facts than do any of the alternative theories.

Briefly, the explanation is this: Transpiration produces a water deficit in the cells of the leaves and, as would be expected, more enters these mesophyll cells by diffusion from adjoining ones. These, in turn, absorb water from their neighbors which are better supplied, and so on until water is drawn from the xylem tubes of the veins of the leaf.

The next step in the explanation calls for an understanding of the way in which the water is held in the xylem. It will be recalled that this tissue is largely made up of tubular cells, and that these tubes are not completely separated from one another. Pits in the walls between adjacent vessels and

tracheids allow water to move more or less freely from tube to tube in various directions. All the water in the xylem therefore consists of a series of slender strands tied together in a sort of network extending from the tips of the roots to the ends of the tiniest veins in the leaves. These strands in the colloidal lignified walls of the xylem tubes do not behave at all like the columns of water in the pipes in a building. One of their peculiarities is that they have great tensile (stretching) strength, something like that of a narrow thread. In fact, these "wires of water" in the xylem of a plant are so strong that they are able to sustain themselves without breaking in even the tallest trees with plenty of reserve strength for much greater lifts. If it were possible to pull an end of one of them, it would be drawn up somewhat at the other end. It is obviously impossible to take hold of such a strand but transpiration does just that. Evaporation takes water from the cells of the mesophyll thus making the solution in the cell sap more concentrate and these cells absorb it from others, until finally a cell replenishes its supply from the end of the column in the xylem of a vein. This action puts the column under a tension that extends to the very root tips, and is relieved only as the roots absorb more.

Along with this straining effect of transpiration on the water columns, there is also a lifting action exerted by roots. Experiments and observations have already been cited (p. 65) to show that the roots help somewhat in the whole process of pushing water up into the stem. Under certain conditions, root tips are able to exert a remarkable pressure—a pressure that has been demonstrated to be great enough to lift a column of water at least 200 feet high. At times when absorption is active and transpiration is not taking place rapidly, root pressure is responsible for much of the water movement in plants. A combination of root pressure (adding water at one end of this system of capillary strands) and transpiration (taking it away at the other) gives what many regard as a satisfactory explanation of the mechanism of the ascent of sap.

When evaporation is very rapid or absorption is slow, almost the entire lifting action depends on the pull exerted by transpiration. When absorption is greatly restricted, as when the soil is relatively dry, or is cold or even frozen, transpiration is correspondingly retarded because of the resistance to water movement exerted by the soil. It is to be understood that the active xylem of the plant usually stands full of water. When absorption fails to keep up with evaporation, the leaves wilt, not because the xylem tubes are empty, but because the resistance in them is so great that diffusion into the living mesophyll cells is greatly retarded. Wilting results from the partial collapse of cells when turgor is reduced.

This knowledge of the water relations of a plant makes it possible to explain another fact which is otherwise difficult to understand. If the stem of a rapidly transpiring plant is cut off, even though it is immediately placed in water, its leaves sometimes wilt. If, however, it is cut under water and the cut end is kept there, the cells remain turgid. Also, a shoot which has wilted can often be revived quickly by cutting off a short piece while the place at which the cut is made is kept under water.

The explanation is that cutting the stem in the air permits the strained threads of water to be suddenly drawn upward, causing air to enter the vessels at the cut end. When the stem is placed in water again, each column in the xylem is interrupted by a bubble which prevents more water from entering. But if it is cut under water, no air enters and the water in the plant remains continuous with the supply. When the stems of the wilted plants are cut shorter under water, the bubbles in the water tubes are left in the parts cut off, reëstablishing the continuity of the water columns.

The Transport of Minerals. Dissolved minerals which diffuse into the roots from the soil and are used in the manufacture of proteins, travel upward mainly through the phloem. The method by which these solutions are carried along is not known, as yet. When proteins are being built, however, nitrates and other soil nutrients are used up, a deficit arises and they tend to enter from without and to travel at a rather rapid rate toward the region in which there is a reduced concentration.

There have been times when it was supposed that these minerals were swept along by the movement of water in the xylem vessels, but it is now known

that relatively small amounts occur in the transpiration stream. Tests of many kinds prove that the transfer of soil nutrients is independent of the upward motion of water through the stem. These experiments in the laboratory are well supported by conditions encountered in the out-of-doors. As an example, observations show that the plants which grow the most rapidly and develop the most vigorously of any in the world are those of tropical jungles which stand full of water, with relatively little loss by transpiration and very little coming in through the roots.

The Translocation of Foods. Most of the carbohydrates and large amounts of proteins are formed in the leaves and apical meristems of plants, but very little food remains in these leafy twigs for any considerable length of time. It is difficult to follow the movements of the proteins, but the behavior of the starches and sugars is fairly well known. Throughout the day, when photosynthesis is rapidly taking place, most of the carbohydrate is stored in the chloroplasts in the form of starch. But when darkness and lower temperature come and photosynthesis ceases, the starch is changed into sugar by the action of enzymes and is carried away.

The channels through which sugars and proteins pass in going to other parts of the plant are not fully understood. Malpighi's experiments first suggested that foods move through the bark, but bark is composed of many kinds of tissues. Experiments have narrowed the search to the phloem as the chief channel of food transfer in the plant. Recent investigations seem to establish the fact that dissolved minerals may travel up in the phloem while carbohydrates are moving down in the same tissue. The structure of the sieve tubes, which are long, wide cells communicating with one another through perforated areas, strongly suggests that they are probably the channels through which foods are carried. These cells usually contain carbohydrates and proteins and there are strong presumptive evidences that this action occurs, although the actual movement of such substances through them has not been observed.

Aeration of Plant Tissues. Not only must every living cell be supplied with water and food, but some oxygen must be available to every living protoplast however deeply it may be imbedded in the body of the plant. In leaves, the intercellular spaces are usually relatively large, permitting oxygen and the other gases of the air to diffuse freely among the cells. In stems and roots of land plants, the intercellular spaces are much smaller, but they are present and form a continuous meshwork of passages through which the air can diffuse to all parts. In young stems and leaves the intercellular spaces connect with the outside atmosphere through the stomata. In young roots the epidermis and outer parts of the cortex are usually much more permeable to dissolved gases than the corresponding parts above the ground, and the air penetrates them more readily. In older stems and roots, where cork replaces the epidermis, the interchange of gases takes place through the lenticels.

Plants like water lilies, cattails, eelgrass, and rice, which normally grow in wet places where their roots are always surrounded by water or wet soil, frequently have much larger and more prominent air spaces. These air spaces are sometimes so extensive and highly specialized that they form a considerable internal atmosphere that is continuous throughout the plant, even to those parts that live entirely under water.

TISSUES CONCERNED WITH SUPPORT. Any thick cell wall adds somewhat to the strength of the structure of which it is a part and if there are numerous walls of this kind crowded together the aggregate mechanical effects of them all may be great. In the various parts of the plant body there are several kinds of cells that appear to have little or no function other than the support which their walls provide. Important among these are collenchyma, sclerenchyma, and wood fibers.

COLLENCHYMA. In the young stem the cells of the outer layers of the cortex often elongate and develop thick, but very elastic cellulose walls. The thickenings of the walls occur especially at their corners. This strengthening tissue is the *collenchyma*. Collenchyma often occurs in leaves as well, being especially prominent in the veins and petioles. Its cells remain alive for a long time and often have chloroplasts, thus playing some small part in the manufacture and storage of food. This function however, is probably only incidental.

SCLERENCHYMA FIBERS. These are long cells with thick, woody walls. They extend lengthwise through the plant and are best developed in the stem and to a less extent in roots and leaves. The protoplasm often forms such thick walls that there is very little room left in which it can live. Then it dies. In stems, where sclerenchyma fibers are usually most highly developed, this tissue may form either in the cortex or in the phloem. That sclerenchyma cells may be extremely strong can be illustrated by the fact that linen thread is made of pure sclerenchyma fibers of the flax plant, cleaned, bleached, and spun.

STONE CELLS. These thick-walled cells are similar to sclerenchyma fibers except that they are not much elongated. They may be found in the cortex of stems, in fruits, and in various other plant structures. The stony layer in peaches, cherries, and various nuts is composed almost exclusively of stone cells, and the sandlike grains often encountered in the fruit of pears are made up of small, isolated masses of them.

STRENGTHENING TISSUES OF THE XYLEM. The majority of the cells of xylem have thick walls and therefore, even the conductive tubes, add a considerable amount of strength to the xylem. In many plants, however, the functions of conduction and strength are to some degree separated, with the water tubes acting primarily as channels of conduction, and the wood fibers furnishing the greater amount of the strength.

STORAGE TISSUES. Foods are produced much more rapidly than they are used by healthy green plants under good conditions, and the excess accumulates in a variety of ways. Annual plants store most of the reserve food in their seeds, thus providing for the nourishment of the seedlings until they become independent in the soil. Biennials, during their first growing season, and perennials at any time, may store food, especially starch, in a variety of places. Almost any living cell in the plant may accumulate food but in general the cortex, the rays, the central pith, and the parenchyma of phloem and xylem are the most important storage structures aside from fruits and seeds.

PROTECTIVE TISSUES. Land plants need protection chiefly from loss of water by transpiration, from the fungi that cause diseases, and from such mechanical injuries as those occasioned by storms and bites of insects. The epidermis shields the young plant from both transpiration and mechanical injury, the leaves and young stem being completely covered by a continuous layer of this tissue. The root is usually well protected by the soil. What is the function of the epidermis of the root?

As the stem matures, cork usually replaces the epidermis, both in location and functions. In some cases, especially in roots just above the root hair zone, the outer layers of cortex become modified and somewhat waterproof, making a *hypodermis* and furnishing temporary protection until the layer of cork, or *periderm*, develops. The epidermis of leaves persists and is not replaced by any secondary tissues.

GLANDULAR OR SECRETORY TISSUES. Probably every living cell is capable of secreting several substances. For example, the very continuation of life requires unceasing respiration in the protoplasm, but respiration depends almost entirely on the action of various enzymes. Still other enzymes bring about the deposition of reserve foods in the cells or subsequently digest them. These various secretions that are active throughout the protoplasm of plants, and probably many others that are not yet known, seem to be organized in all the cells where they carry on their functions. In this sense the entire plant might be considered to be a gland.

Besides these enzymes and other substances that are formed throughout the plant, there are others that are produced in rather definitely localized glands. Probably the most important of these glandular structures, so far as the welfare of the plant is concerned, are the growing tips of shoots (see p. 44). A few examples will illustrate the importance of their secretions.

If a potted plant that is producing flowers and a succession of flower buds is transferred to a dark room the buds cease to develop within a few days and soon wither or fall off. If, instead of placing the entire plant in the dark, all growing tips with their youngest leaves are effectively darkened by means of small black caps, the same results occur even though the mature stems and the older leaves are exposed to the sun. These experiments demon-

Long-day and short-day plants. (Courtesy, Boyce Thompson Institute, Yonkers, N. Y.)

strate the fact that some kind of flower-producing secretion, as yet not fully understood, forms in young, leafy stem tips; that it is not secreted without the stimulus of light; and that it does not develop in the older parts of the plant even when they are exposed to direct sunshine. This flower-producing hormone has been called *florigen.* In some way, when florigen is present in proper amounts the apical meristem organizes floral structures instead of leaf primordia.

PHOTOPERIODICITY. In many plants flowering is sharply seasonal. Such seasonal behavior is commonly called *periodicity.* As examples, cultivated cosmos and chrysanthemums blossom in the fall when the days are becoming short. During the long days of midsummer these plants commonly grow vigorously but do not produce flower buds. If, however, their periods in the light are artificially shortened to about twelve hours by keeping these plants in the dark during a part of the time, flowering can be induced even in summer. For some reason *short-day plants* do not secrete florigen except when their days are less than 12 or 13 hours long. Other well-known short-day plants are asters, salvia, nasturtium, poinsettia, wild strawberries, and violets. Some of these bloom in the spring and others in the fall but always when the daily exposure to light is short.

Others, the *long-day plants,* produce flowers only in the longest days of midsummer. Such common field and garden crops as oats, wheat, timothy, clover, beet, spinach, lettuce, and radish belong to this class. Shortening the period in which these plants are exposed to light, by placing them in the dark or by fitting black caps over their growing tips stops the production of florigen, and flowering soon ceases. By such artificial means long-day plants can be caused to continue to grow without the production of flowers for many months or even years. On the other hand, these plants can be induced to produce flowers even in the shortest days of winter if their day is lengthened by even a weak artificial light. In this way, if a few electric lights sometimes of even very low wattage are kept burning during a part of the night in a greenhouse in winter, thus supplementing the short period of daylight, and extending the total period of illumination to 16 or 18 hours per day, the long-day plants will produce flowers.

Some species, such as the pansy and the common annual sunflower, are *neutral* as to length of day, blooming at any time when conditions suitable for growth permit.

The periodicity exhibited by many plants is of considerable economic importance, as when the expert florist controls the time of blooming of his plants that must be ready for market on certain specified days of the year. Such control is usually brought about largely by supplementing the length of day with electric lights during a few hours of the night. It is interesting to note in passing that many plants are damaged if they are not subjected to darkness during at least a few hours of the twenty-four.

SECRETION OF AUXINS. A well-rooted plant in a flowerpot may often be killed by being trimmed back behind the last of the active, growing buds and leaves, even though numerous dormant buds are present. Under similar conditions, however, the same plant is likely to thrive if the cutting is taken above, instead of below, even a small active bud. The explanation of this difference in behavior is that in the first case, the dormant buds produce little or no auxin and growth therefore does not take place, leaves do not develop and the plant starves as soon as its food reserves are exhausted. In the second example, the growing meristem with its young leaves produces growth substances, permitting the normal development of a vigorous shoot capable of secreting a continuous supply of auxins and of carrying on photosynthesis. Just what effect light has on the apical regions of young stem tips when it stimulates them to secrete florigens and auxins is not yet understood.

OTHER GLANDS. Many plants have glands that are much more definite and clear cut in form than the rather diffuse ones thus far described. Mention has been made (p. 118) of the digestive glands on the leaves of sundew and Venus' flytrap, and of those that line the resin ducts in the wood, bark, and leaves of many of the gymnosperms (p. 105). Other examples are those that secrete the pungent oil in orange peel. These can be seen easily without magnification, as crowded translucent spots as

large as small pinheads on any part of the surface of an orange. The pleasant odor of geraniums is produced in specialized, rounded microscopic cells on the outer ends of some of the epidermal hairs. Likewise, the flavors of many plants such as the mints, parsley, and cloves, as well as the characteristic odors of various flowers are almost all secreted in more or less well defined glands.

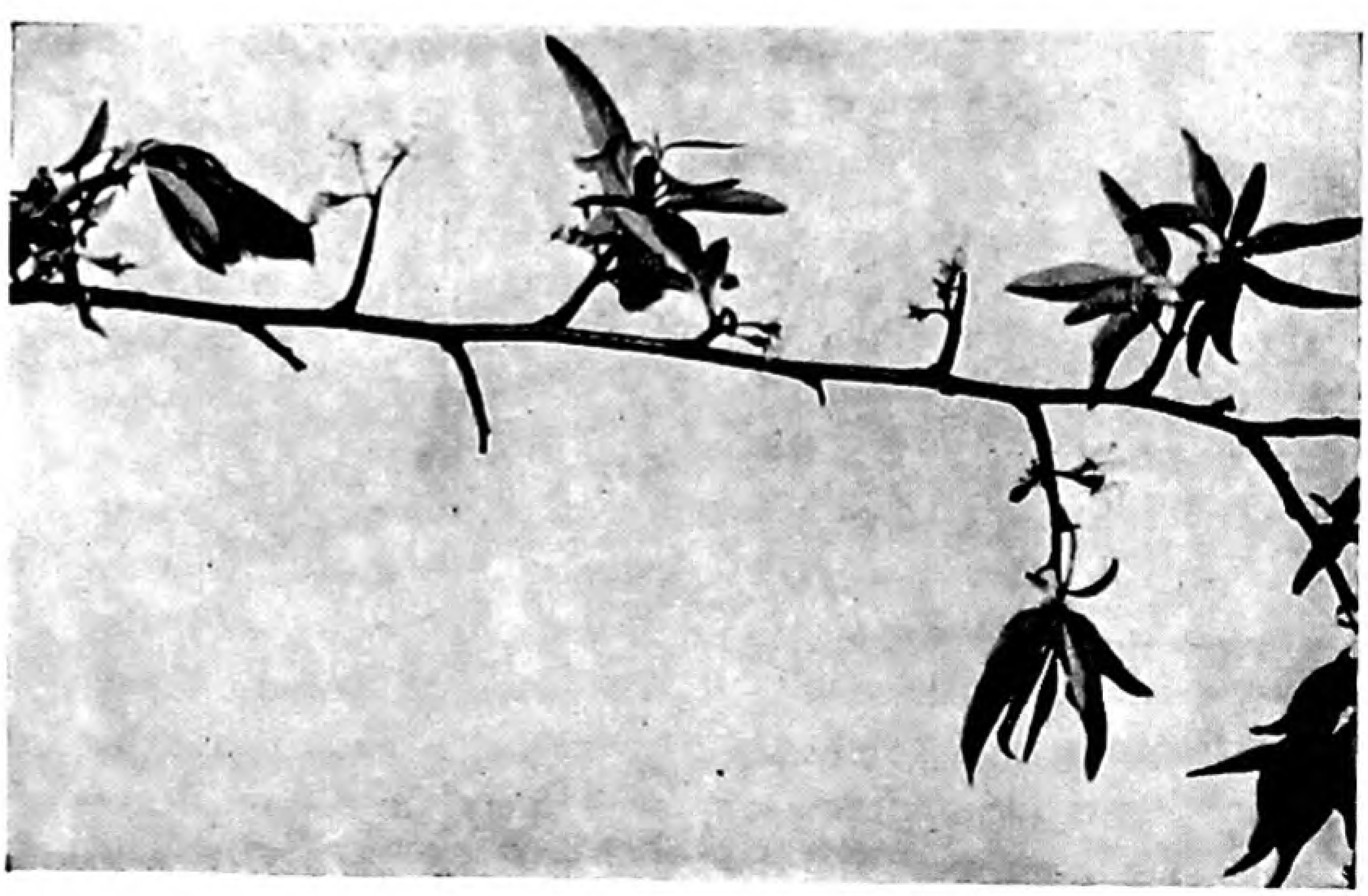
LATEX VESSELS. Many kinds of plants contain appreciable amounts of milky juice known as *latex*. Among the best known of these are the milkweeds and spurges, members of the poppy family, the morning-glory and its relatives, the mulberries and figs, the Osage orange, the India rubber tree, some of the sumacs, dandelion, lettuce, and chickory.

The latex in these plants is located in special tubes known as *latex vessels*. Although the exact condition in some plants is not well known, it seems that there are at least two types of these vessels. In one, illustrated by the poinsettia or by the India rubber tree, they are formed by the breaking down of partitions in series of cells which are arranged end to end. That is, they develop in much the same way as the water tubes in the xylem. In the dandelion and some of its near relatives, on the other hand, certain cells differentiated from the meristems have the ability to grow and push their way for long distances among the other tissues. The tubes formed in this way frequently join others and finally come to be a complicated network. In either type these tubes extend into almost every tissue of the plant. Just how the milky juice is formed and what its functions may be in the life of the plant are not fully understood.

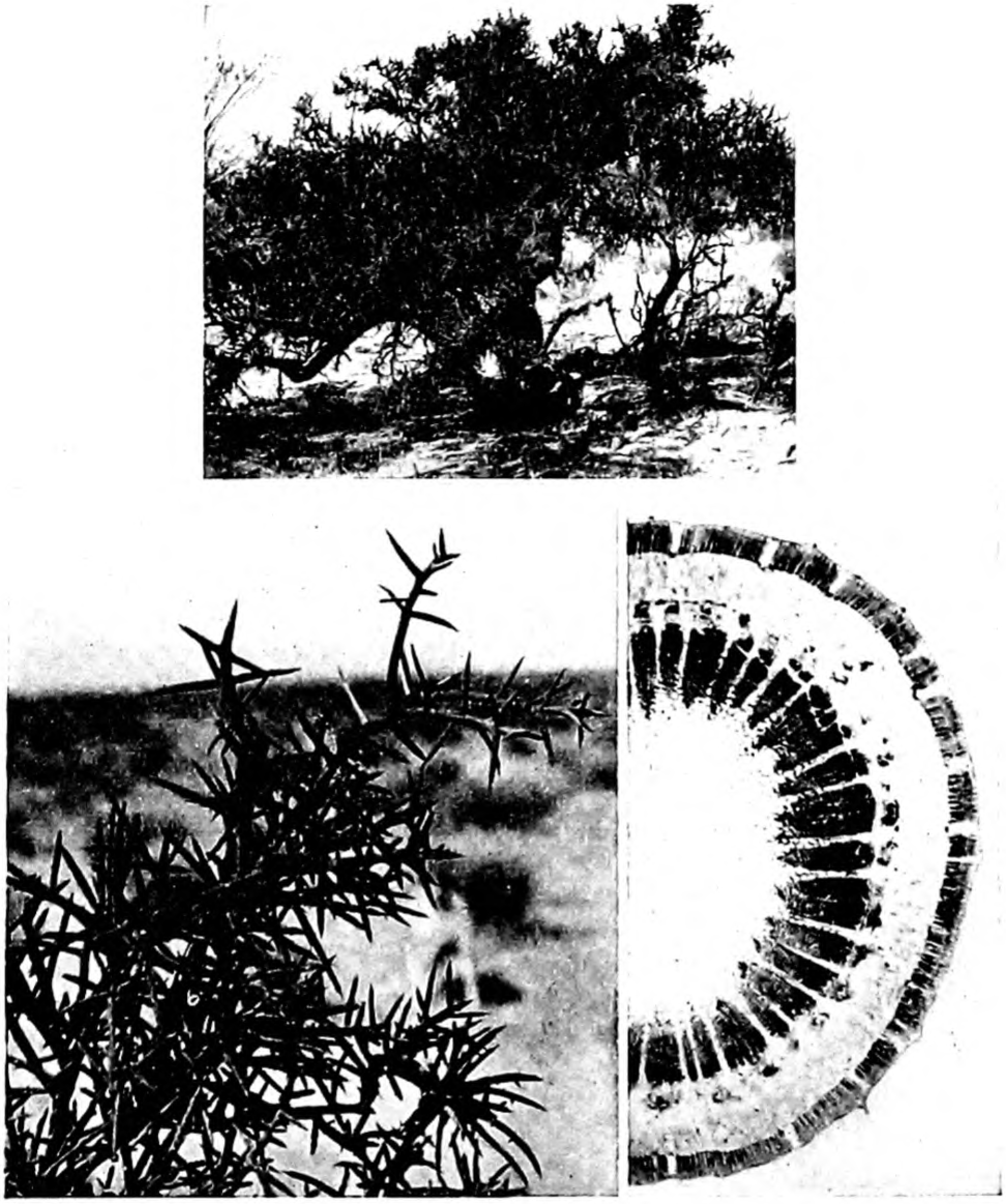
Latex is used commercially in the manufacture of numerous products. That which is produced by the India rubber plant and a number of other species is heated or treated with acids, making crude rubber, which is changed by various treatments into the different kinds used in manufactured articles. The latex of certain members of the sumac family is the foundation of lacquers and varnishes; that of the poppy family and a number of other plants contains large amounts of opium and similar narcotics; and still another is used in the manufacture of chewing gum.

ANOMALOUS STRUCTURES. After the usual tissues of root, stem, and leaf have been examined, there still remain some parts of certain plants that seem to have been overlooked. A few of these will be interpreted below. In almost all cases a careful study of either their position or the way these peculiar structures differentiate from the meristem shows them to be highly specialized forms of ordinary tissues or organs. As an example, a *thorn* is actually a woody stem that tapers to a hard, sharp point.

A careful study of the thorns of such woody plants as red haw or some kinds of wild apples or wild plums reveals many distinctive stem characters. Externally, nodes are frequently clearly marked by small leaves or by leaf scars. These thorns are located at the tips of branches or develop in a lateral position in the axil of a leaf. Those of honey locust trees almost always have several branches, which frequently arise in an axillary position. From one to several large, compound leaves often grow on these giant many-pronged thorns, still further emphasizing the fact that they are really highly specialized stems.



Thorns. Branch of plum tree with flowers and leaves on short branches that are forming thorns.



Allthorn. (*Top*) A large individual. (*Bottom, left*) A branch, showing stemlike character of the thorns. (*Bottom, right*) Cross section showing stem structure. Note that the outer cortex takes the form of palisade tissue. Near Alamogordo, New Mexico.

Thorns, spines, prickles or some combination of them are especially common on woody plants of desert and semiarid regions. In such places there are sometimes almost impenetrable thickets of armed shrubs and small trees.

One of the most extreme examples of a thorny desert shrub or small tree is that of allthorn (*Koeberlinia spinosa*) which is fairly common in certain parts of the Southwest. Its stems branch and rebranch in a very intricate manner, always ending in powerful, incredibly hard, sharp tips. Its only leaves are minute scales, so small that they are likely to be overlooked except with careful scrutiny. The cross section of a thorn, however, clearly shows the characteristic structure of the stem of a dicotyledon with its central pith, surrounded, in order, by zones of xylem, cambium, phloem, cortex, and epidermis. The greatest difference between these stem structures and the corresponding ones of many other dicotyledons appears to be that most of the cell walls of the thorns are extremely thick and hard.

A *spine* is a modified leaf or a part of a leaf. Those of such plants as some of the barberries show their

leafy character in two ways. First, each is located on a stem below a bud or a branch in the place where a leaf should be; and second, a perfect series of structures extending from true spines to normal leaves can readily be found in at least one species of barberry. The spines of some plants, including the black locust, mesquite, and a considerable number of other members of the pea family, seem to be modified stipules since they are located in pairs at the base of each petiole. Those of ocotillo, a desert shrub of the southwestern United States, are the hard, sharp, persistent midribs of old leaves.

A *prickle* is a sharp outgrowth from the superficial tissues of a stem or a leaf. Roses, blackberries, raspberries, gooseberries, and many other plants have scattered prickles variously arranged over their surfaces. When they are removed they are found to

Spines forming from leaf midribs in ocotillo. Tucson, Arizona.

Prickles on stem of wild rose.

arise from the epidermis or from a combination of epidermal and cortical tissues.

A *tendril* is a specialized outgrowth from a stem or leaf that coils around any available support as can be seen from the illustration on p. 113.

The petioles of the leaves of clematis and nasturtium often make one or more turns around a suitable support, acting as tendrils, although they are only slightly specialized. Actually, these are ordinary leaf stalks with a highly developed thigmotropic response.

VEGETATIVE PROPAGATION. The ordinary vegetative organs such as roots, stems, or leaves of many

species readily form adventitious roots and shoots. By this means new plants come from old ones by simply continuing the development of tissues and organs that have been organized previously.

Runners of Boston fern.

The various kinds of *stolons* are the commonest and most effective means of vegetative propagation. Some of these are only slightly specialized stems. Take, for example, the slender stems of some of the blackberries, raspberries, and sedges, that grow upward for a time and then arch over until the growing tip touches the ground, strikes root, and establishes a new plant. Others, such as strawberries, cinquefoils, and numerous grasses, have specialized stems which extend horizontally over the ground. Some of these produce roots at the various nodes while others root at the growing tip only. These prostrate stolons are often called *runners*.

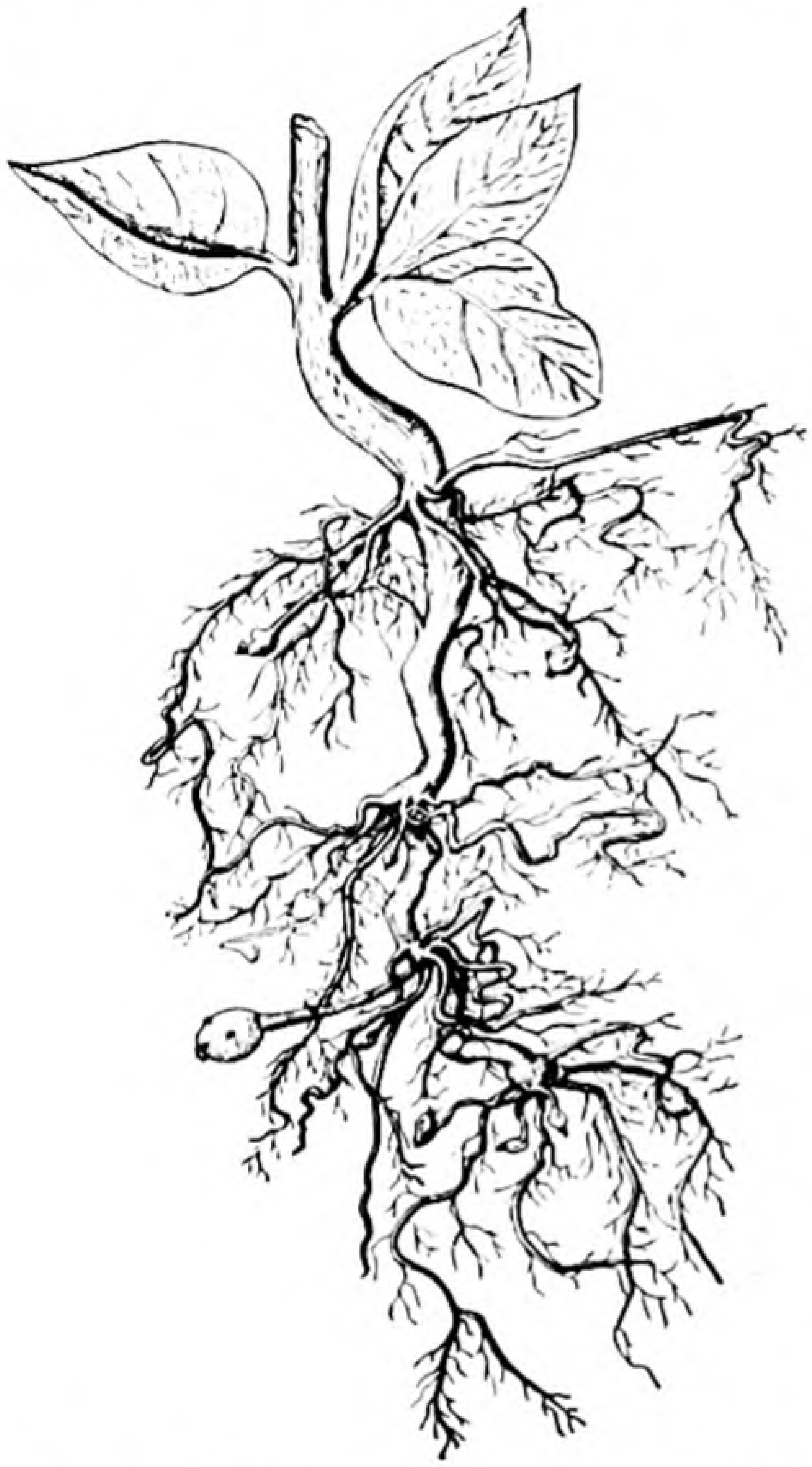
A great many plants have more or less elongated, usually horizontal underground stems, which are essentially subterranean stolons from which adventitious roots grow into the soil and aerial stems or leaves extend into the air. Such underground stems are called *rhizomes*. Good examples are to be found in Solomon's seal, iris, most ferns, and many grasses. The identity of a rhizome can usually be readily established by the fact that it has more or less definite nodes and rudimentary leaves of some sort, usually with axillary buds (see the illustrations on pp. 87 and 90).

Closely allied to rhizomes as organs of propagation are certain horizontal roots of plum trees, white poplars, tree-of-heaven (*Ailanthus*), staghorn sumac, and a number of other thicket-forming trees and shrubs. These roots give rise, adventitiously, to new plants at more or less frequent intervals.

FLESHY ORGANS OF STORAGE AND PROPAGATION. The thickened, usually underground, parts of many plants which function as storage organs for food, and occasionally for water, are sometimes roots and sometimes stems. In any case, most of them play important roles in the propagation of these plants. When such a structure is a modified underground stem it is known as a *tuber*. One of the best examples is the common potato. It begins its development as a short rhizome with a few scale leaves and a terminal bud covered by leaf rudiments. As food accumulates, the outer end enlarges, and the buds in the axils of the rudimentary leaves become the "eyes," the subtending leaves themselves being the eyebrows. When potatoes are planted, the buds grow, forming the new plants.

Strawberry stolons. The small plants at the right and left developed from the tips of stolons (runners) produced by the older, central plant.

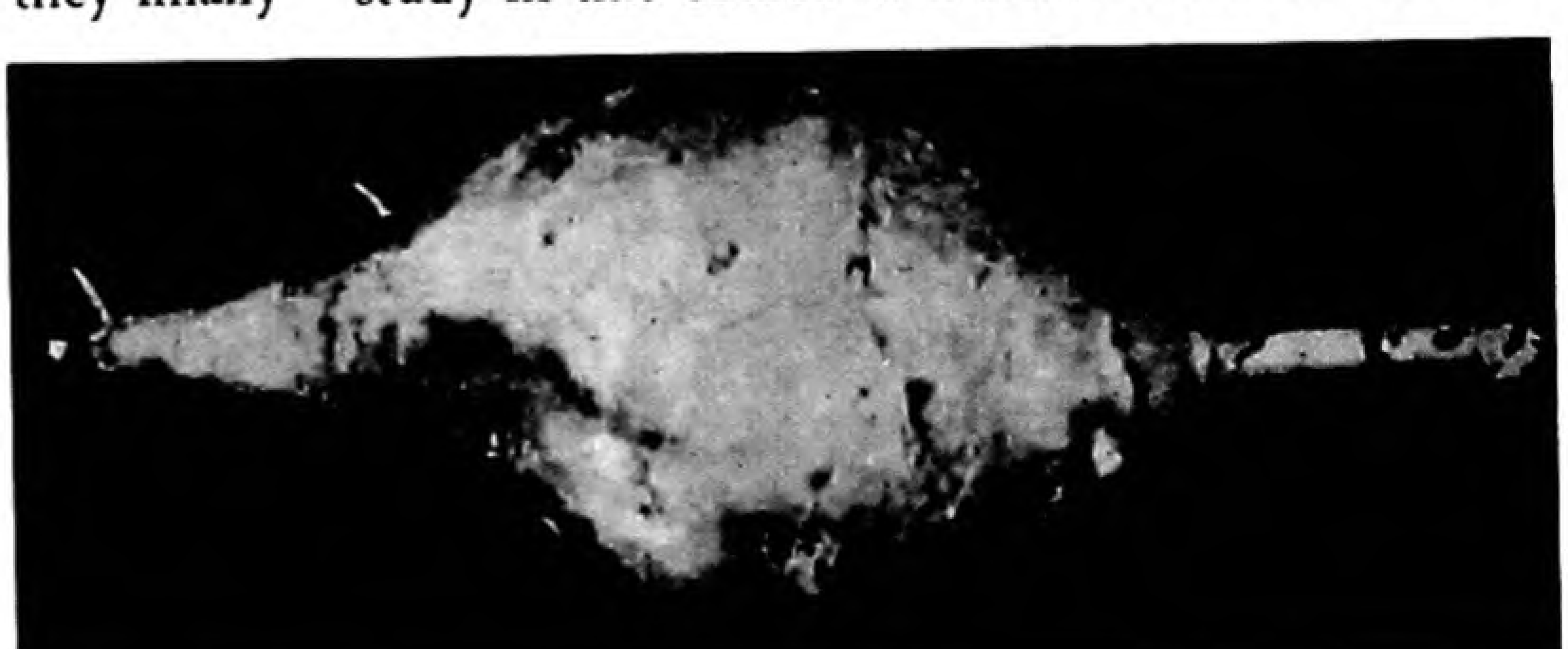
By way of contrast, the swollen underground parts of the sweet potato plant are *fleshy roots*, sometimes called *root tubers*. They first appear as small adventitious roots growing from the sprawl-



Potato plant with fibrous roots and with young rhizomes beginning to swell into tubers at their outer ends.

ing vine where it touches the ground. They gradually become less rootlike in appearance as they enlarge with accumulating food until they finally take on the irregular, tuberous, mature form. As organs of propagation, these fleshy roots give rise to adventitious roots and shoots, establishing new plants.

Such plants as crocus, gladiolus, and Jack-in-the-pulpit have short, thick, vertical, solid, bulb-like underground parts more or less enveloped by thin, papery leaf bases. A fleshy organ of this kind is known as a *corm*.



Fleshy root of sweet potato.

A true *bulb* has the well-known arrangement of parts of a dry onion or lily bulb. It consists of a very short, conical stem usually tipped by an apical meristem, and surrounded by a number of thick, fleshy scale leaves. At least a part of these leaves have buds in their axils, and it is from them that the new bulbs arise. A bulb is very much like a large bud rooted at the base.

UNUSUAL MEANS OF PROPAGATION. The "walking fern" shown on p. 77 takes its name from its peculiar habit of producing new plants on the greatly elongated tips of its leaves. These tips often grow in length, extending as slender protrusions, sometimes several inches long, from the outer end of the leaf blade. When they come in contact with moist soil they organize roots and leaves which are capable of repeating the process.

A considerable number of species of cacti have jointed stems that frequently drop some of their sections. These pieces become scattered, produce roots, and grow. Even the fruits of some of them, falling to the ground, grow into new plants.

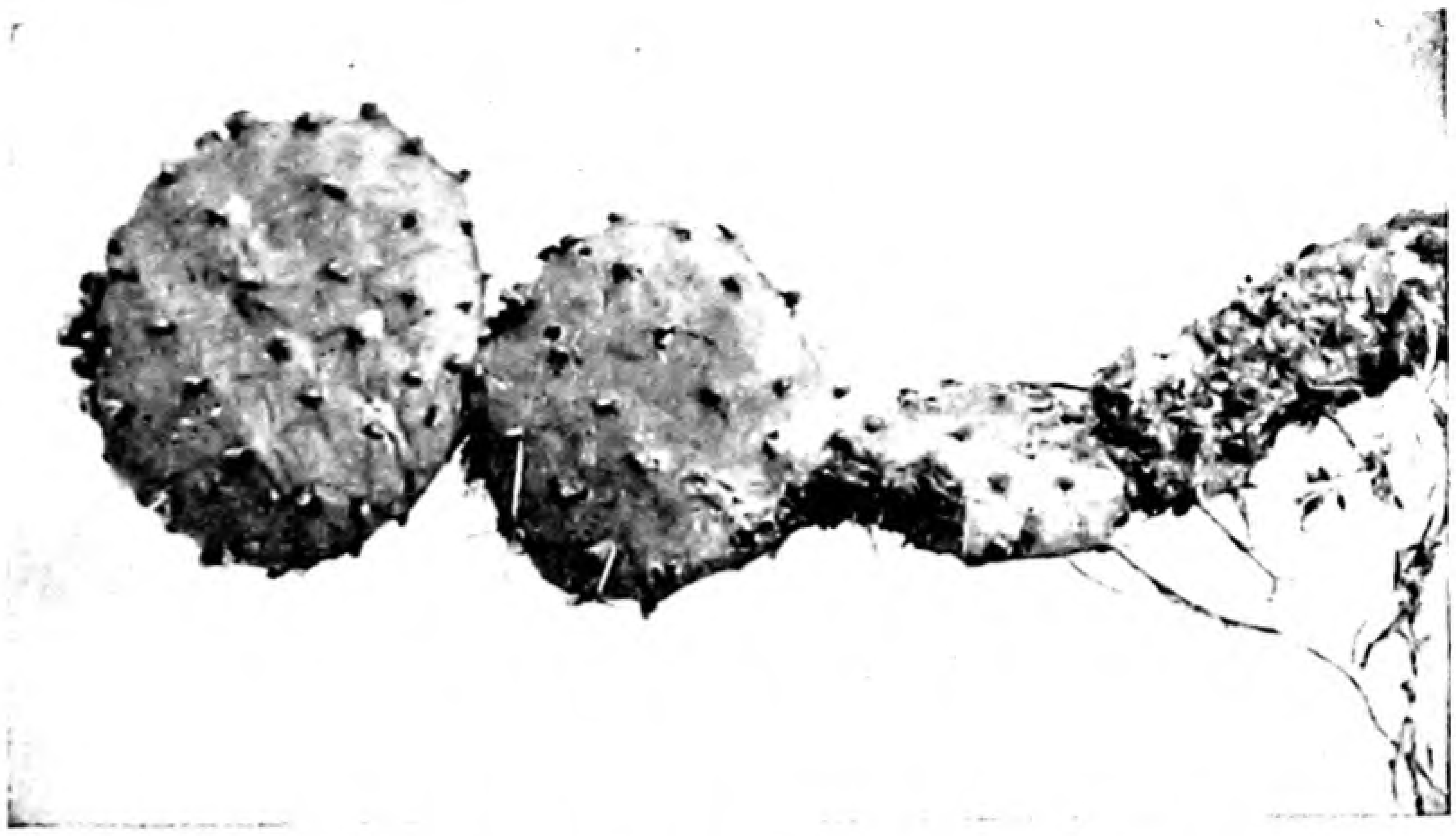
The detached leaves of some house plants such as *Bryophyllum* produce new roots and shoots at their notches whenever they come in contact with moist ground and in the closely related *Kalanchoe*, well-formed plantlets organize while the leaves are still growing on the stem.

Numerous other cultivated plants such as *Saintpaulia* (African violet), *Sansevieria*, and some of the begonias can be propagated by covering the petioles or parts of the blades of the leaves with moist sand.

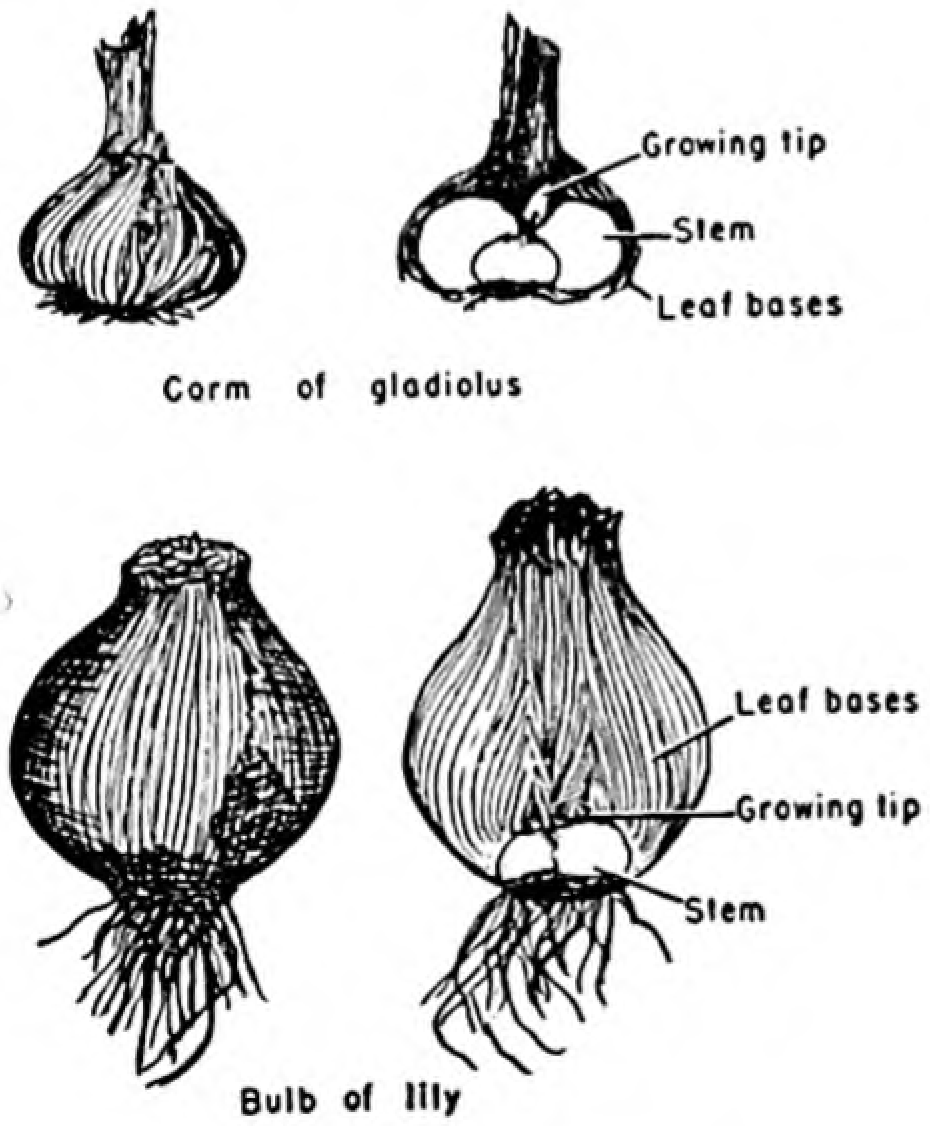
Summary. This chapter is intended to cause the student to synthesize into one unit all previous study in this course as it relates to the individual

plant and to see the entire organism as a living, growing structure; to see the threads of anatomic and physiologic similarities extending throughout the plant body; to gain some comprehension of the unifying effects of hormones and other secretions; and yet to see clearly the minor contrasts which distinguish the various parts and types of the higher plants.

All these types of growth forms and reactions of plants illustrate the larger fact that living protoplasm is sensitive to its surroundings and is so constructed that its activities change considerably in response to differences in its environment. Such responsiveness is called irritability. Chemical and physical changes may bring about differences in activity of a formative nature, such as different absorption rates, different thicknesses and types of cell walls, and differences in secretions and, therefore, of digestion, respiration, and general metabolism. The most obvious responses are the tropisms in which various plant organs bend or change direction of growth under the influence of external stimuli.



Prickly pear cactus spreading by forming adventitious roots on the flat, jointed stem.

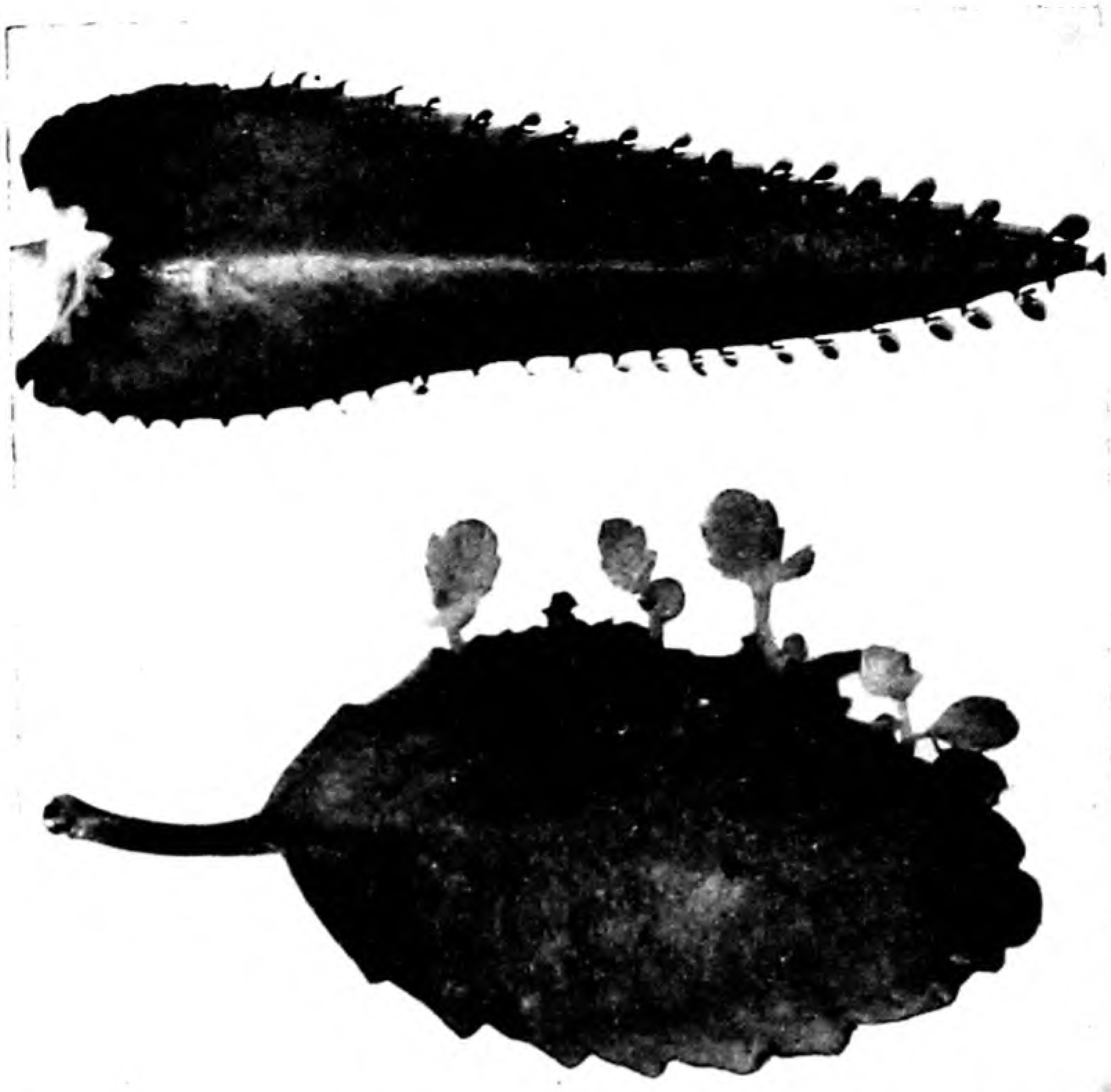


Bulbs and corms.

Not only do the parts of a plant act together as a unit but they are also constructed as a functioning whole. In previous chapters various structures and activities of the plant have been examined as if each were separate and independent. Such analysis is necessary in dealing with complicated structures and processes because it is impossible at first to comprehend the picture as a whole. But the plant does not live in fragments; it is more than an assemblage of individual cells carrying on independent processes. It is an organism composed of many coöperating cells and tissues, each performing its group of functions. In order more fully to understand this fact, we should now fit together the different parts and processes and see the plant in its entirety.

As an aid, the student should set a plant before him, recalling in detail all the structures, materials, and activities that have been studied. A clear mental image should be called up by each of the following: apical meristem, assimilation, bud, cambium, chloroplast, collenchyma, companion cell, cortex, diffusion, digestion, endodermis, enzyme, epidermis, gene, hormone, metabolism, mitosis, node, osmosis, palisade, parenchyma, pericycle, phloem, photosynthesis, respiration, root, root branch, root cap, root hair, sclerenchyma, sieve tube, stele, stem, stoma, tracheid, transpiration, vein, vessel, wood fiber, and xylem. Any points that cannot be clearly brought to mind should be reviewed until every important structure and process can be imagined in its relations to all the rest of this living plant.

This exercise should be carried out with such precision that the plant becomes a wonderful unit



(*Top*) Leaves of *Kalanchoe* and (*bottom*) *Bryophyllum* producing plantlets at the notches.

in mental perspective. Questions like the following may help to this end: What parts of the plant have epidermis? If some parts do not, what takes its place? What form does the cortex take in root, stem, and leaf? What functions is each of these parts of this plant performing at this time? What would result if one of these functions or structures should be discontinued?

SUPPLEMENTARY READINGS

Avery, *et al.*, "Hormones and Horticulture."
Bonner and Galston, "Principles of Plant Physiology."
Curtis and Clark, "Introduction to Plant Physiology."
Hayward, "The Structure of Economic Plants."
Kains and McQueston, "Propagation of Plants."

Chapter 10

PLANT GENETICS

A corn plant is different from a pumpkin vine; a fern is not like an oak tree; an alga is distinct from a sweet pea. Behind the scenes there is at work an orderly set of controls collectively called heredity. These controls cause the offspring of the oak to be oaks and of the pumpkin to be other pumpkins.

But no two oak trees and no two pumpkin plants—in fact, no two organisms of any kind are exactly alike. It is the small differences between closely related forms that are most useful in interpreting heredity and for this reason the study in this chapter will be limited to an examination of a few simple, easily recognized distinctions. Nevertheless, the knowledge gained in this way forms a solid foundation on which all subsequent work in this course will be built.

The following outline of this chapter will serve to give direction in mastering some of the most important principles that underly plant genetics:

- How Heredity Acts
  - Mendel's Experiments
  - Monohybrids and Dihybrids
  - The Mechanism of Heredity
    - Sexual Reproduction
    - Mitosis
    - Meiosis
    - Gametophytes and Sporophytes
- Chromosomes and Genes
- Phenotypes and Genotypes
- Unusual Chromosome Behavior
- Genes in Action
- Applied Genetics
- Heredity and Environment

Some cultivated four-o'clocks have white flowers, some have pink, and others red. Hybrids, produced by crossing white varieties with red ones, have pink flowers, but two pink ones crossed with each other are likely to have offspring with all three colors—white, pink, and red. Not only will these colors be present but they appear in the definite relative numbers, or ratios, of two individuals with pink flowers to one with red and one with white. This ratio is approached more closely as numbers become larger. That is to say, if there are only four individuals produced by such a cross the numbers are only rarely two pink with one of each of the other colors, but if there are 4,000 the numbers are certain to deviate only slightly from 2,000 pink-flowered plants and one thousand each of red and white.

How Heredity Acts. It has been observed for centuries that closely related individuals resemble one another sufficiently to suggest that certain characteristics have been transmitted from ancestors to offspring, but that offspring may fail to show some peculiarities which their parents had and, on the contrary, may have some which their

immediate ancestors did not have. This whole matter of the transfer of characteristics from generation to generation is known as *heredity*, and the science which attempts to understand the process is called *genetics*.

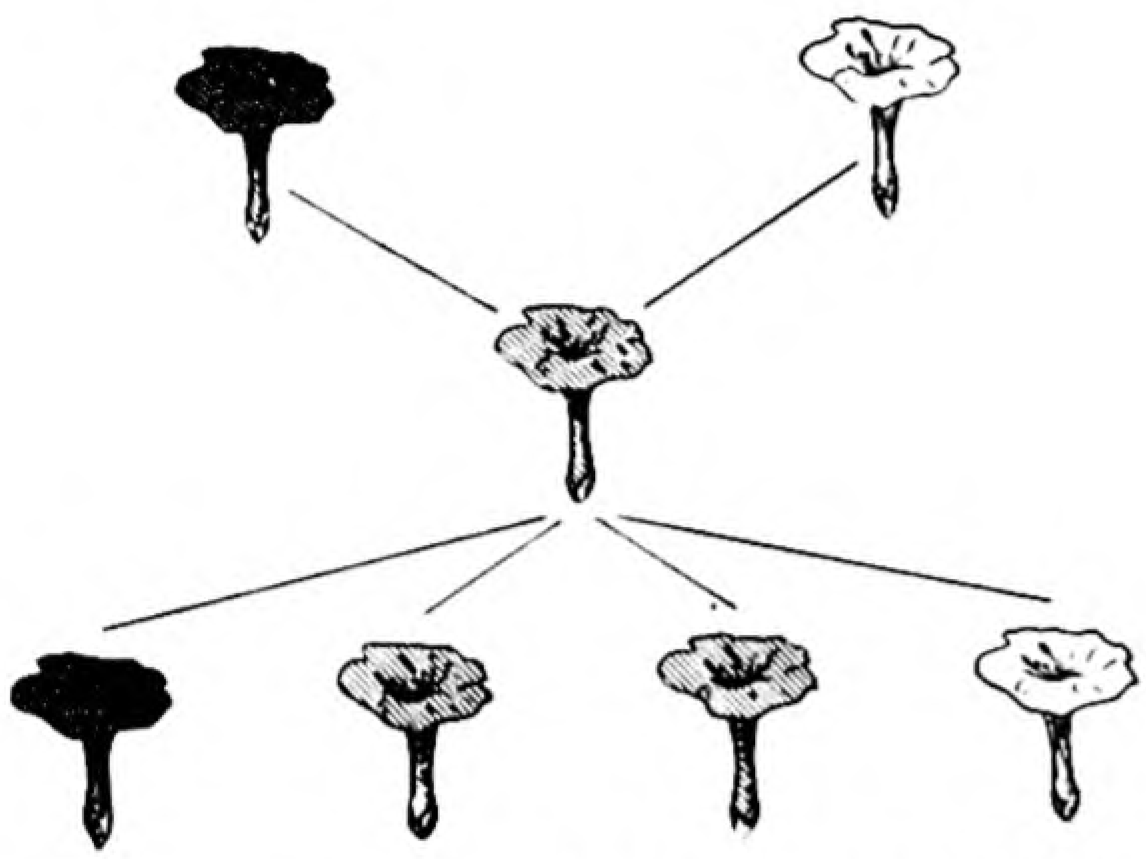


Diagram illustrating the characteristic 1:2:1 ratio found in four-o'clock flower colors.

MENDEL'S EXPERIMENTS. As a beginning step in making an analysis of the complicated action of heredity an important experiment will still further illustrate some of the basic facts involved. This experiment was carried on about three-quarters of a century ago by an Austrian monk named Gregor Johann Mendel, one of the pioneers in discovering the laws of genetics. For his study he chose two pure strains of garden peas, one of which was tall and the other short. He produced hybrids between them by placing the pollen from members of the tall variety on the stigmas of members of the short or bush form. Conversely, he pollinated flowers of tall peas with pollen from short plants. He chose these characteristics because he wanted to experiment with clearly contrasting, measurable features, for it is obvious that a plant grown from a seed produced in this way could not be both tall and short at the same time. To his astonishment Mendel found that whether the seeds grew on tall or short individuals, all the plants grown from these hybrid seeds were as tall as the taller parent. By some means tallness had completely obscured any tendency to assume the short form. Mendel described this behavior by saying that in the pea tallness is *dominant* and shortness is *recessive*.

A *hybrid* is a cross between parents that differ in at least one characteristic. The offspring in such a cross is called the F_1 or first filial generation (*filius*, a son). A cross between two members of an F_1 generation results in the F_2 generation.

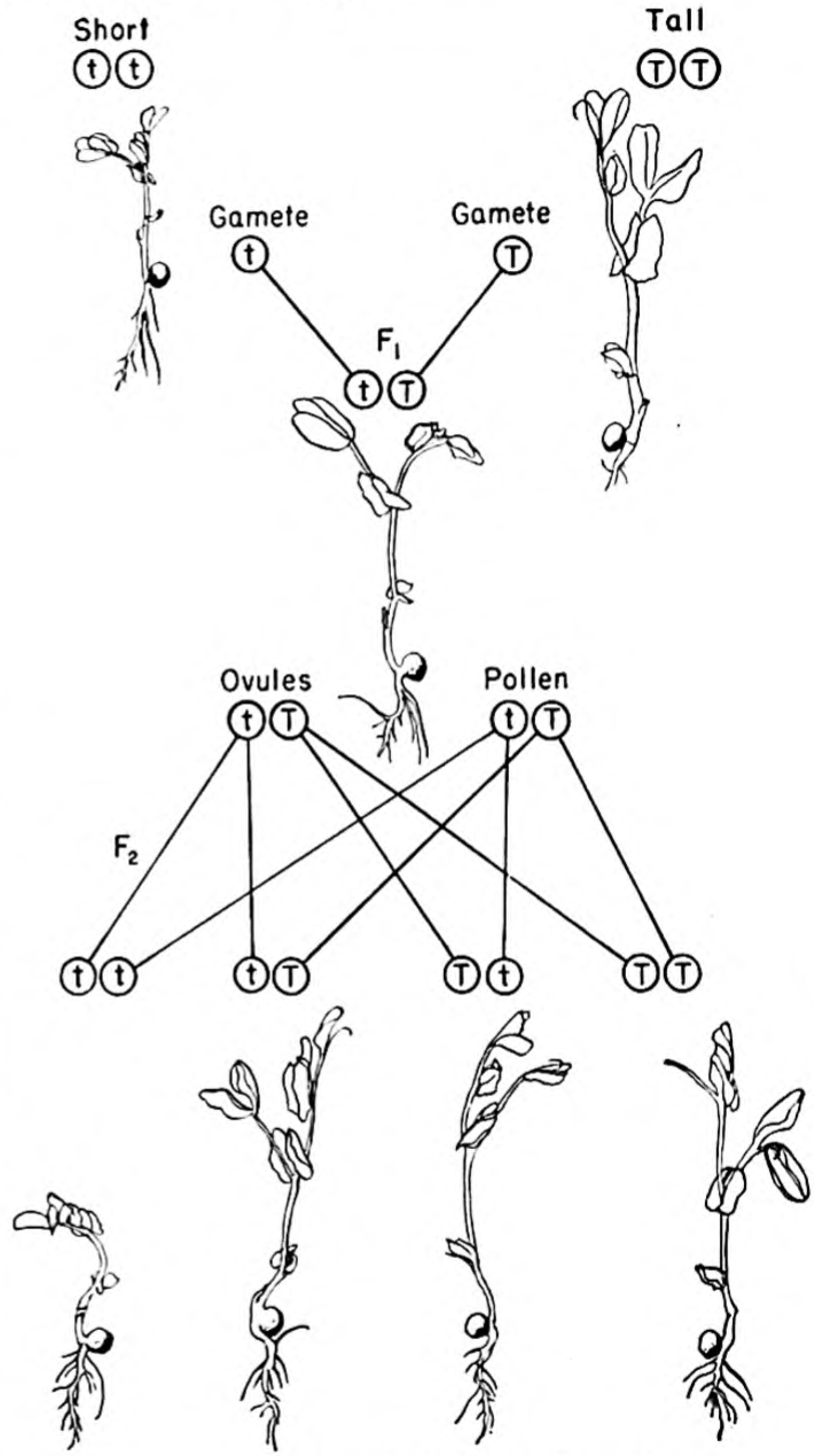


Diagram illustrating Mendel's experiment in which he studied inheritance in tall and short peas. (T) Tall-producing gene. (*t*) Short-producing gene.

The F_1 hybrids just described were all tall. These were next crossed with themselves (selfed). When the resulting seeds were planted the next year,

three-fourths of the F_2 plants grew tall and one-fourth were short. In other words, they appeared in a ratio of 3 tall : 1 short.

Each of these plants, both the tall and the short, was selfed and once again the seeds were planted. In this case all the short peas and one-third of the tall ones bred true, while the remaining two-thirds of the F_2 tall peas produced offspring in the ratio of 3 tall : 1 short.

This can be stated in another way: All the short plants were pure stock so far as the character of shortness was concerned. This statement is proved by the fact that if the pollen from a short pea plant is placed on the stigma of a short plant all the resulting offspring are short. Likewise, those tall peas all of whose inbred offspring were tall were pure for that character. On the other hand, the remaining half of the F_2 plants, that is, those whose inbred offspring appeared in a 3:1 ratio were hybrids in as true a sense as were the F_1 hybrids.

If tallness and shortness had been the only characteristics that behaved in this manner this series of experiments would have had little actual value. But Mendel made similar crosses that involved a considerable number of other contrasting characteristics such as colors of flowers, colors of seeds, smoothness and wrinkledness of seeds, and positions of flowers on the plant. In all of these experiments he found one characteristic of a pair that acted as a dominant over the other, and in all cases the ratios were similar to the ones described above. Such similarity of behavior in crosses of so many kinds was strong evidence that some fundamental process was at work. Succeeding paragraphs will gradually clarify the basic meaning of this statement.

(It is convenient at this point to introduce a term which Mendel did not use but which is now widely employed in genetical work. Two contrasting characteristics, such as tall and short stems, yellow and green seeds, or smooth and wrinkled seeds, are known as *allelic characters*, or simply as *alleles*. These terms will be used in all future discussions.)

A second important fact which Mendel discovered was that hereditary factors behave as *independent units*. These units have been referred to frequently in earlier chapters under the name of *genes*. A proper study of the figures and of the various examples given in the discussion show that during the succession of generations, the members of each allelic pair reappear in as definite form as if they had not been associated with their alleles in the hybrid.

Ideas of *dominance* and of *independent units*, together with a third, usually referred to as *segregation*, have come to be called Mendel's Laws. The meaning of segregation can be seen by studying the diagrams once again, for although any given hybrid will have determiners for both members of an allelic pair, in later generations these alleles separate or segregate, entering into the constitution of different individuals. Briefly, then, *Mendel's laws mean that independent genes come together or segregate freely in the generations, and that one is dominant over the other.*

Although Mendel's laws apply almost perfectly in the experiments he carried out in discovering them, in the light of later work with other hybrids some shift of emphasis must be made to keep these laws in agreement with observed facts. Thus, the experiment described in the opening paragraph of this chapter illustrates a variation from the situation as seen in the characteristics just described in peas. The colors of the four-o'clock flowers illustrate the fact that heredity is transmitted from generation to generation in the form of independent genes which segregate in the usual way. But in contrast with the characters studied in peas, one of these alleles does not entirely overshadow the other, that is, dominance is not complete. This type of action is now known to be very common and is described as *incomplete dominance*. Many degrees of incompleteness occur in both plants and animals.

MONOHYBRIDS AND DIHYBRIDS. These experiments have dealt with a single set of alleles at a time, and the F_2 generation has always shown the ratio of 3:1, as in the pea, or a variant of it, 1:2:1, as in flower colors in four-o'clock. This is known as the *monohybrid ratio*.

When two sets of genes, instead of only one, are followed through a series of crosses, what appears superficially to be a more complex ratio occurs in the offspring. In fact, however, each pair of alleles

produces its own ratio and the apparent complexity is only the result of a combination of two simple ratios. This situation can be illustrated by a combined study of tallness and the color of pea seeds. The genes which produce tallness and shortness are alleles as are those which cause yellow and green seeds. Either of these allelic pairs gives the monohybrid ratio when used alone. If a plant of pure stock which breeds true for tallness and has green seeds is hybridized with a short plant having yellow seeds, the F_1 plants are tall and the seeds are yellow because of dominance in both characters. Self-pollination produces in the F_2 generation all possible combinations of these characteristics in the following ratio: 9 tall yellow:3 tall green:3 short yellow:1 short green. This ratio, 9:3:3:1, is known as the *dihybrid ratio*. Careful inspection of the accompanying outline reveals the fact that each allelic pair follows the monohybrid 3:1 ratio. In

3 tall : 1 short
3 yellow : 1 green

9 tall yellow: 3 short yellow: 3 tall green: 1 short green

Dihybrid ratio in pea, showing that this ratio is the result of combining the monohybrid ratios for tallness and for color.

the same way, the *tribybrid ratio*, 27:9:9:9:3:3:3:1, results from the use of three sets of alleles. Other ratios are secured with larger numbers of alleles, but they are of little value in the elementary study of most genetic problems because they are too complicated to be useful.

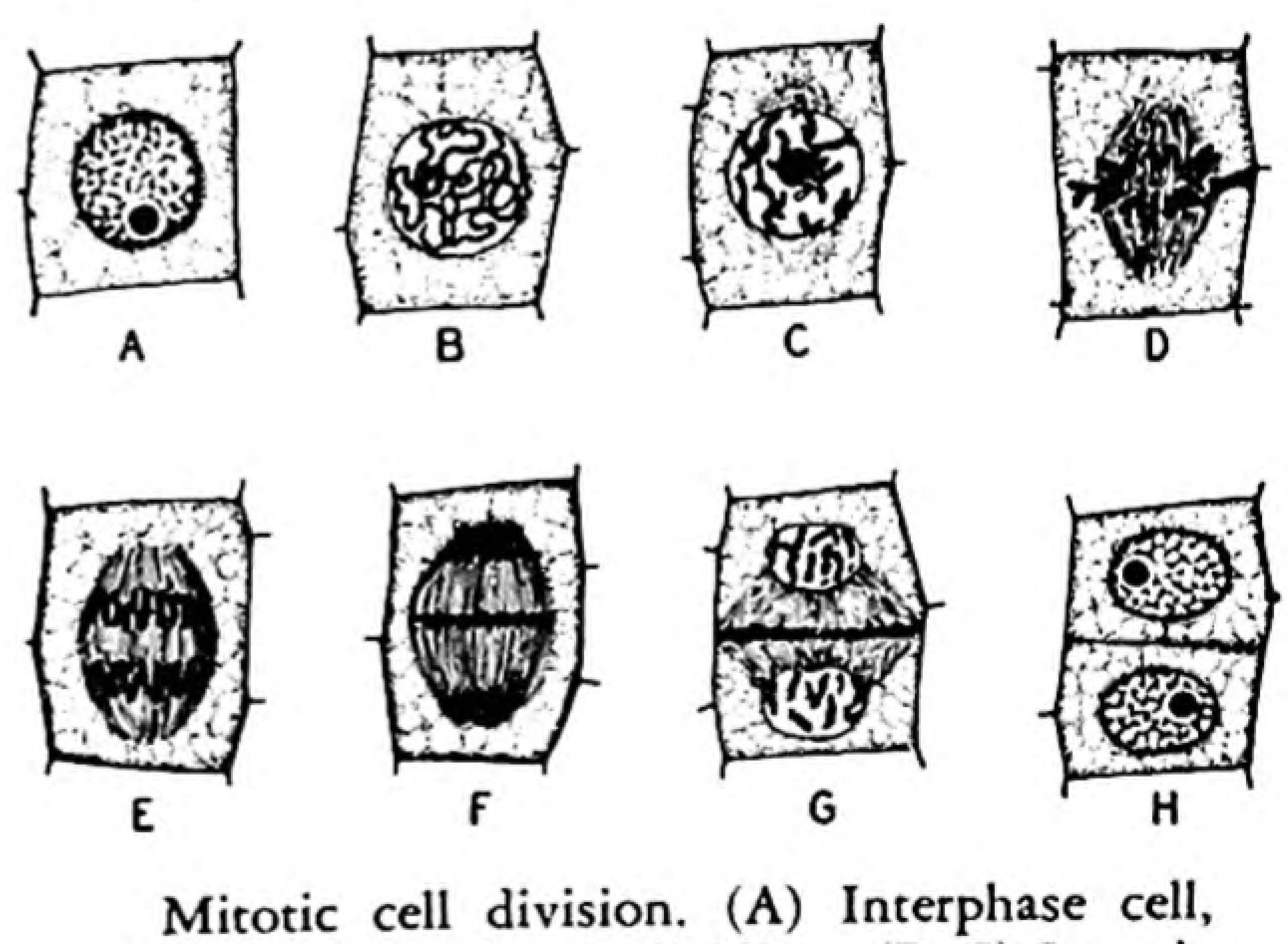
THE MECHANISM OF HEREDITY. Experience has shown hybridization, that is, the making of crosses between organisms that are somewhat diverse from each other, to be the best approach to the study of heredity. Hybridization always involves sexual reproduction.

SEXUAL REPRODUCTION. In all sexual reproduction two specialized cells, called *gametes*, unite to form one cell, the *zygote* (*zygotos*, yoked). The uniting of gametes is called *fertilization*. In the case of angiosperms—the most extensive studies of plant genetics have been made with these—the two gametes are very different from one another. The larger one, produced by the female parent, is the *egg*, and the smaller comes from the male and is called the *sperm*. In many species of plants both sexes are present in one individual, but in these, the same ratios and principles of heredity are displayed as when the sexes are separate.

In order to understand both genetics and growth it is necessary to have clearly in mind a complete outline of chromosome behavior throughout the life history of a common plant from the time it is a zygote until it has become mature and has produced offspring.

In fertilization each gamete brings to the zygote a half set of chromosomes. Therefore the zygote receives a full set, half from each parent. Soon after fertilization the zygote divides, forming two new cells. This division is the beginning of a series by which a considerable mass of tissue is built up, all descended directly from the zygote. This body of cells forms inside the developing seed and is called the *embryo*. It is the embryo that grows eventually into the new plant, other parts of the seed disappearing soon after germination takes place.

MITOSIS. The nuclear changes involved in the cell division incident to the usual growth processes are called, collectively, *mitosis*. In properly stained tissues observed at high magnification, the resting



Mitotic cell division. (A) Interphase cell, i.e., a cell that is not dividing. (B, C) Steps in prophase. (D) Metaphase. (E) Anaphase. (F, G) Steps in telophase. (H) The two daughter nuclei and the young daughter cells.

or interphase nucleus, that is, the nucleus in which mitosis has not begun, is seen to have the following parts: the *nuclear membrane*—an extremely thin layer of protoplasm enclosing the rest of the

nuclear material; inside this the *nuclear reticulum*—a network of specialized protoplasm which contains the *chromatin;* a central *vacuole;* and at least one *nucleolus* imbedded in the body of the nucleus.

When a cell is beginning to divide, the nuclear membrane soon disappears, and the nuclear reticulum becomes organized into long, slender threads which gradually shorten and become thicker, and finally form a group of bodies—the *chromosomes* (*chroma*, color; *soma*, body). In living materials the chromosomes do not have color but are transparent, although they can be seen to some degree with proper magnification. In the preparation of permanent slides intended for study with the microscope, the tissues are first treated with chemicals that very quickly kill the protoplasm and coagulate it so that it does not change shape. Then, certain dyes that stain the chromatin are used. Hence the bodies containing chromatin have come to be called chromosomes.

In the living, dividing cell the chromosomes gradually split lengthwise, but the two halves or daughter chromosomes, called *chromatids*, remain for a time attached to one another. The changes taking place up to this time are called the *prophase*. In the *metaphase*, which follows immediately, these double chromosomes group together near the equator of the cell. At about this time the nucleolus gradually disappears and a *spindle* forms, composed of large numbers of *spindle fibers*. These fibers converge toward the ends, or poles, of the cell. There is much doubt as yet as to the function of the spindle fibers. In fact, there is some evidence that they simply mark lines of tension that develop in the cytoplasm. At the end of the metaphase the daughter chromosomes separate from each other, are moved away from one another by means of some force not yet fully understood, and travel to the opposite poles. This migration is called the *anaphase*. The *telophase* follows at once with the organization of the two new sets of chromosomes into two daughter nuclei.

At about the time of the telophase a primary wall usually forms between the new nuclei, completing the mitotic division of one cell into two similar ones. Direct microscopic observation shows that the intricate processes of cell division may be completed in various plants in from 30 minutes to a few hours. This series of steps is repeated millions of times in the meristems of a growing plant, and all the complexity of a fully developed seed plant arises from the specialization of groups of cells produced in this manner. By tracing mitotic division from beginning to end it becomes evident that each daughter cell has the same number of chromosomes as the cell from which it was derived. Therefore, every cell of a plant body has the same number. In fact, each species has its own characteristic number, as a few examples will illustrate: canna, 6; trillium, 12; pea, 14; onion, 16; sweet clover, 16; milkweed, 20; lily, 24; tulip, 24; pine, 24; oak, 24; and jimson weed, 24.

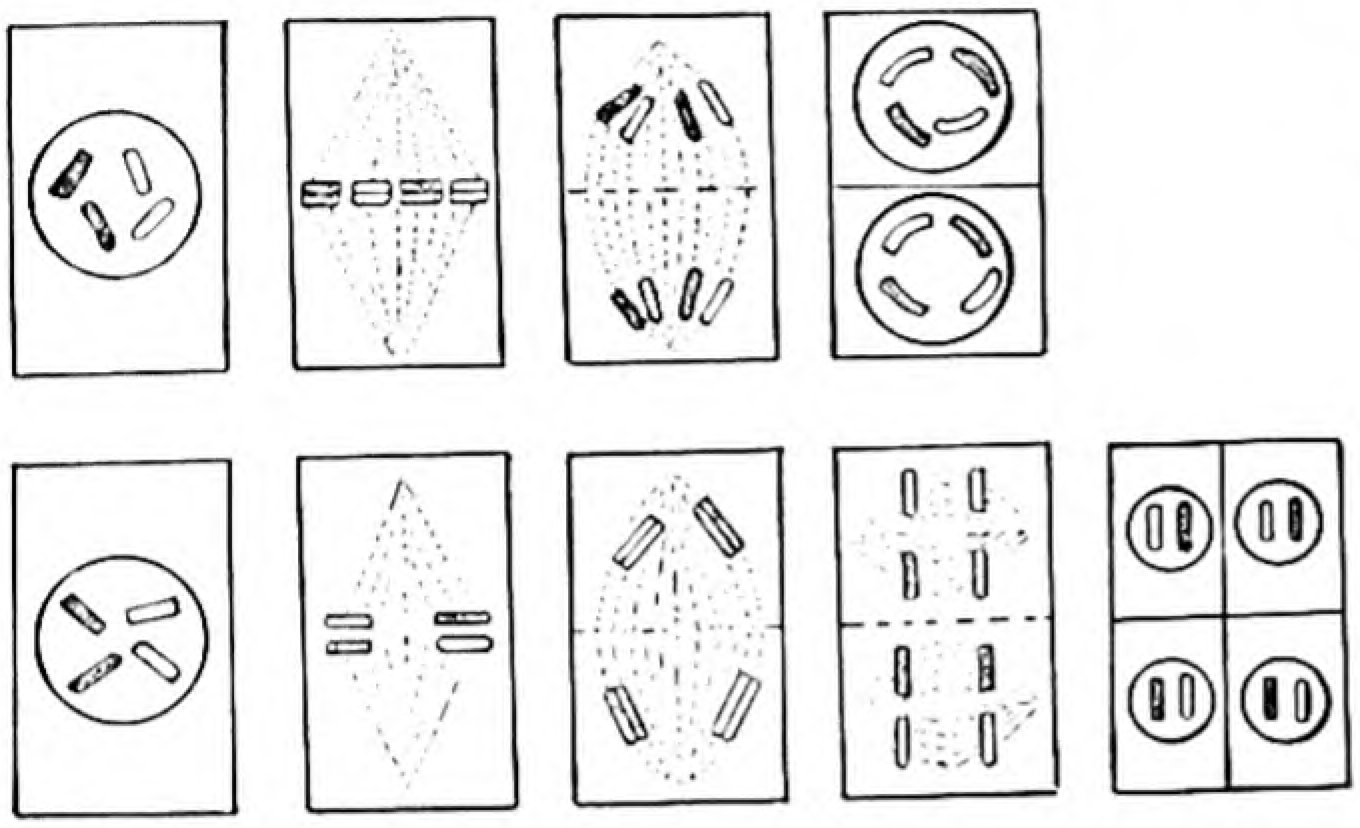
It is enlightening to note that all these numbers are divisible by two. The reason is that each kind of chromosome appears in duplicate in every cell, the two members of a given pair coming originally from the two parents of the plant. The significance of these paired chromosomes will be emphasized in the succeeding paragraphs.

MEIOSIS. Since each gamete contributes its set of chromosomes in the formation of a zygote, the sexually reproduced organism would double the size and complexity of its nuclei with every generation if there were not some action which reduces the chromosome numbers. Instead of such endless duplication, however, a *reduction division*, often called *meiosis* (*meion*, smaller), occurs in the life history. In the angiosperms, while the flower bud is taking form, certain cells in the developing anthers (pollen-producing organs) and others in the ovules (structures that give rise to seeds) enlarge and change in appearance. These are the *spore mother-cells*. It is these cells that undergo reduction division or meiosis.

The steps taken in meiosis are fundamentally the same as those in mitosis until the metaphase is reached. At this stage the chromosomes are seen to be paired and instead of half chromosomes, or chromatids, the whole members of these pairs separate and migrate to the poles. This action divides the number of chromosomes by two. One other division, this time of the mitotic type, follows, keeping the reduced number and bringing about the formation of four cells. From these cells a *tetrad* (*tetra*, four) of spores is formed. The spores in the anther of a flower are usually called

pollen grains. Those in the ovule do not have a corresponding common name.

GAMETOPHYTES AND SPOROPHYTES. The reduced or *haploid* number (*haploos*, simple) of chromosomes is often indicated as n, and the doubled number, or *diploid* (*diploos*, double) as $2n$. The diploid refers to the two sets of chromosomes in the zygote and the plant that develops from it, and the haploid to the number following reduction division.



Diagram, contrasting mitosis and meiosis. In mitosis, *above*, each daughter cell has exactly the same kind of chromosomes as that of the cell from which it was derived. In meiosis, *below*, each of the four cells of the tetrad has only half as many chromosomes as the mother cell from which they were derived. (*Left to right*) The stages are spore mother-cell; pairing of chromosomes; halves of these pairs migrating to poles. It will be noted that at this stage the chromosomes are beginning to split, preparatory to the next step, which is separation and migration of split chromosomes; and finally, formation of tetrad of spores, each of which has the reduced number of chromosomes.

Both the spores which are haploid, and the zygotes which are diploid, are capable of mitotic division, thus maintaining their characteristic chromosome numbers in all cells arising from them. In this way the zygote gives rise to an individual with $2n$ chromosomes in each cell, and the spore to one of a different kind with n chromosomes.

At this point it should be understood that these two, one developed from a spore and the other from a zygote, are actually two different generations, each performing its specific function in the life history. The haploid individual is small, sometimes even microscopic, in seed plants.

Haploid plants characteristically produce gametes. For this reason they are called gametophytes (*phyton*, plant) or the *gametophyte generation*. The microscopic gametophytes that develop from the pollen grains produce sperms. Therefore they are *male gametophytes*. *Female gametophytes* with their eggs form in the ovules. Both the sperms and the eggs have n chromosomes.

Diploid plants, that is, those that develop from zygotes, characteristically produce spores and are called *sporophytes*.

SUMMARY TO THIS POINT. It is profitable now to summarize the discussion by saying that in fertilization the egg and sperm each contributes its haploid set of chromosomes, producing a zygote with duplicate sets. By repeated mitotic divisions, the cells are formed that are to become organized into the diploid sporophyte body; finally, meiosis brings into existence the haploid gametophyte which produces gametes. The top diagram on p. 143 illustrates the manner in which the chromosomes (and with them the genes) are distributed through the processes of mitosis, meiosis, and fertilization in a normal, complete life history.

Genes. It is evident that the microscopically small gametes do not possess such actual body characteristics as the size, shape, and color which they transmit from generation to generation. Instead, the gametes contain active chemical substances or protoplasmic structures which in due time cause the body characteristics to develop. These determiners of heredity are technically known as *genes*.

Chromosomes and Genes. Early in the century it became clear that the genes, although this term had not yet been given them, followed exactly the same pattern in the genetic experiments as that followed by the chromosomes in the growth and reproduction of plants. Out of a recognition of this similarity of distribution, together with a number of other related discoveries, came the theory that the chromosomes carry the genes and that wherever the chromosomes go, the genes go with them. Such a mass of supporting evidence has now been compiled that practically all biologists of the present day are convinced that this concept should now be considered, not as a theory, but as an established fact. In some cases, the actual spots on certain

chromosomes at which specified genes reside have been determined.

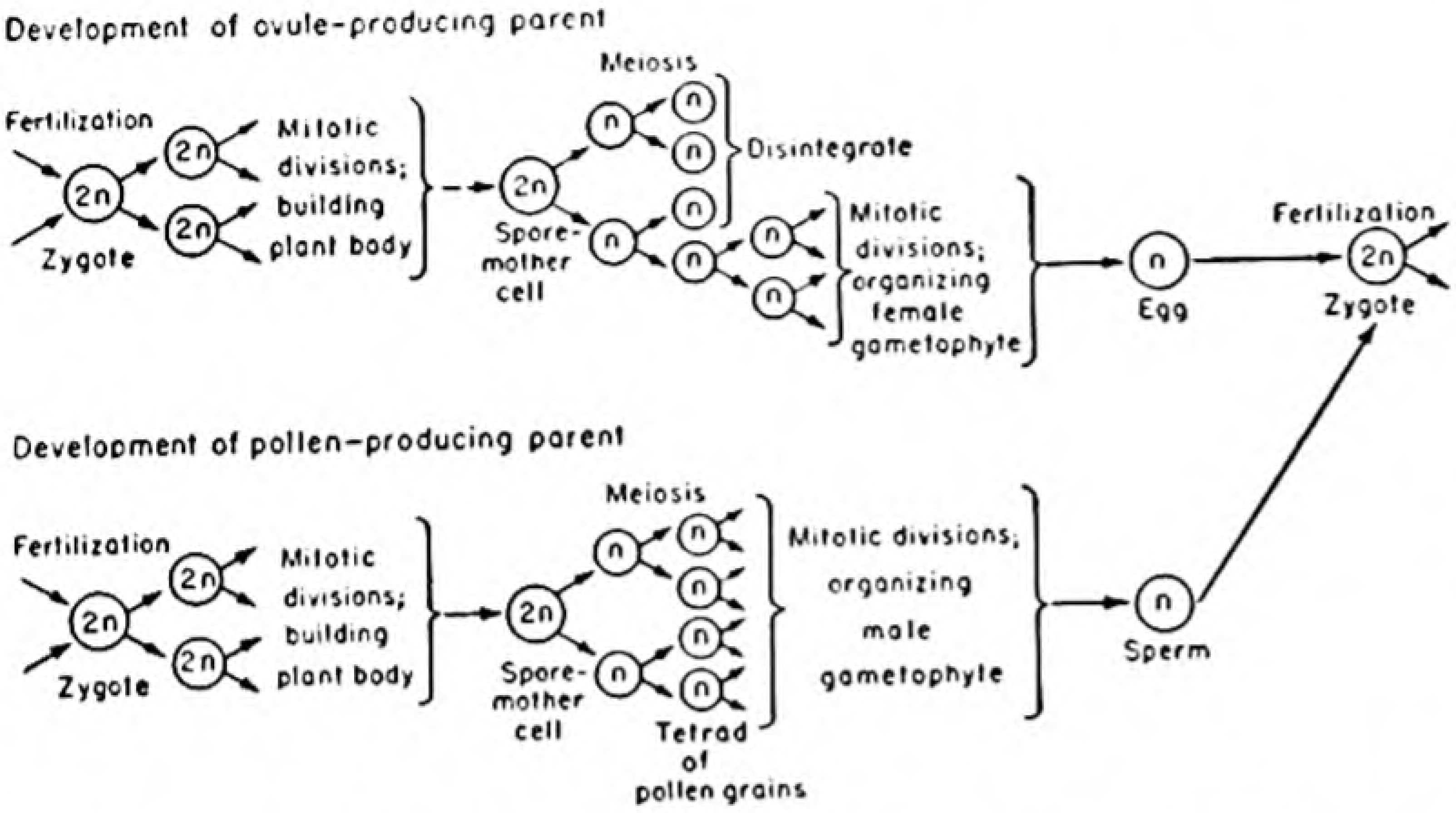


Diagram tracing chromosome numbers through a complete life cycle of a seed plant. (n) One set of chromosomes. (2n) Two sets of chromosomes.

THE CHROMOSOME. When one examines chromosomes as they appear in the usual microscope slide prepared to demonstrate them, they seem to be dark threads or rods with no structure inside them. Investigators, however, have found that other methods of staining can show details which are not visible in the ordinary preparation. Thus it has been discovered that the chromosome is made up of two parts, an outer *matrix* and the thread which it encloses, the *chromonema*. During prophase this thread takes on a spiral form, shortening and thickening the entire chromosome. At about the same time the chromonema either splits lengthwise or duplicates itself. In either case it takes on a double form, a condition which is evident in metaphase. At telephase the chromonema uncoils, becomes diffuse, and enters into the structure of the new nuclear reticulum, only to reappear in the next prophase. The chromonema is variously interpreted as a series of genes in orderly sequence or as a structure to which the actual genes are attached. There is general agreement, however, that the gene itself is either a large molecule of nucleoprotein, derived from sugar, phosphate, and nitrogen compounds, or perhaps a collection of such molecules. Whichever proves to be true, there is increasingly convincing evidence that the effects of genes come about from their capacity to organize enzymes and through them to control the various details of metabolism. Thus the change of a single gene (mutation) in corn brings about the production of an oxidase which destroys auxin, resulting in a dwarf plant with the same number of internodes as is possessed by the usual tall form. The plant produces the auxin only to destroy much of it.

One other feature should be made clear at this point. Every organism that has been investigated thoroughly has large numbers of genes. In some plants and animals the numbers prove to be very great—even hundreds and thousands. In these same organisms there are only a few pairs of chromosomes. Obviously each chromosome must carry a considerable number of genes. This conclusion is supported by the observed fact that certain groups of characters tend to be inherited together. As an example, yellow corn usually has a red cob and white corn a white cob. Likewise a strain of corn has been discovered in which purple grains are similarly associated with shredded, ragged leaves. Such grouping together of characters or their genes is called *linkage*. There are the same number of *linkage groups* as there are of chromosome pairs in any given species.

Phenotypes and Genotypes. The words *phenotype* and *genotype* are two terms that have been coined to express new knowledge which has been gained since the days of Mendel. The term phenotype (*phainein*, to show) means the visible and measurable characteristics of hybrids. Phenotypic ratios are expressed in descriptive terms. Thus, Mendel found in his F_2 cross between tall and dwarf peas that the ratio was 3 tall: 1 dwarf. This is a phenotypic ratio.

Genotypic ratios, on the other hand, refer to the transmission of the genes from one generation to the next and are somewhat different from those of the phenotypes. Illustrating from the same example, and using the customary symbols to represent the genes that control height the following statement may be made: A pure tall pea has two similar genes commonly represented by the capital letters, *TT*. These genes correspond closely with

what Mendel called unit characters. Clearly, they are not characters, however, but determiners that cause the characters to appear. In like manner the pure dwarf peas have the genes, *tt*. The small letters stand for recessives. In genotypic terms, therefore, the parental crosses in Mendel's experiments would be expressed as $TT \times tt$.

As stated above, one of Mendel's laws is that of segregation. It is now possible to restate this law in modern terms by saying that in the production of gametes *only one gene of an allelic pair can appear in a given egg or sperm*. Hence, when the parent carrying the determiners *TT* produces gametes, only one gene, *T*, can be present in a given egg or sperm. In like manner each gamete from the dwarf plant carries the gene, *t*. If an egg containing the gene *T* is fertilized by a sperm containing the gene, *t*, or vice versa, the fertilized egg, or zygote, and the resulting offspring will have the formula *Tt*.

Because of dominance the hybrid plant will be phenotypically tall, with the genotypic formula, *Tt*. When these hybrids produce gametes, half of the eggs and half of the sperms carry the gene *T* while the other half carry *t*.

When Mendel made crosses between such hybrids there resulted the surprising ratio which he found. The reasons are not difficult to understand. The following diagram indicates the possible chance combinations and the ratios in which they may be expected to occur.

Since the gene *T* is dominant and since three-fourths of the offspring in the F_1 receive this determiner while one-fourth does not, the reason for the phenotypic ratio of 3 tall:1 short is obvious. But the genotypic ratio is $TT{:}2Tt{:}tt$. These genotypic symbols may be read, 1 *homozygous dominant*:2 *heterozygous*:1 *homozygous recessive*. The term *homozygous* means that the two genes of an allelic pair in the zygote are alike (*homo*, same) and *heterozygous* means that they are unlike (*heteros*, other). The ratios 3:1 and 1:2:1 refer to the same plants, but the genotype tells what genes are present and therefore what to expect of the offspring, while the phenotype only describes the appearance of the present generation.

When the genotype of the parents in a cross is known it is easy to compute the probable combinations that will appear in the offspring if a sufficiently large number of these individuals is examined. For example, an interpretation can be made of the cross described on p. 154 in which a pure strain of short peas with yellow seeds is

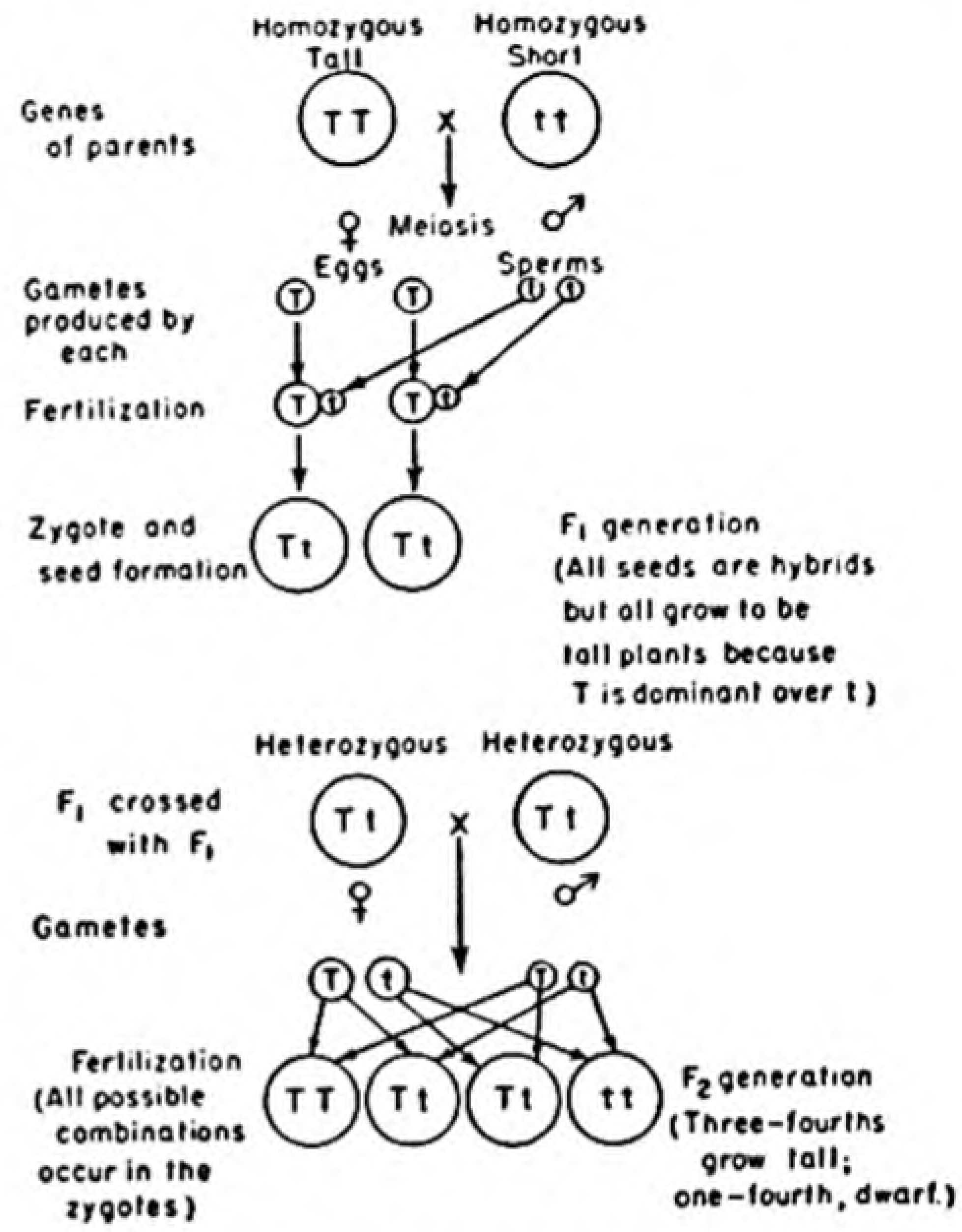


Diagram tracing the genes for tallness in peas through the F_1 and F_2 generations, showing the reasons for the ratios that occur.

hybridized with one that is tall and has green seeds. The symbols for the genes can be expressed as follows: the genes for tall and yellow, being dominants, will be represented by *T* and *Y*, respectively, while their recessives, short and green, will be given the symbols of *t* and *y*.

Since these are pure strains they are homozygous for both sets of genes. In other words, the same gene appears twice in each cell and a translation of the phenotypic characteristics of the parent plants into genotypic formulae reads as follows:

$$\begin{array}{cc} \text{short yellow} & \text{tall green} \\ tt \quad YY & \times\ TT \quad yy \end{array}$$

Tracing the genes that control tallness and shortness in these plants while disregarding those that have to do with color, the genotypic ratio reads

$$tt \times TT \rightarrow Tt$$

Translated into words, this means that all the off-

spring from this cross are heterozygous. Because of dominance, the plants are phenotypically tall.

The situation is exactly duplicated in the case of seed color, the genotypic pattern of the cross in this case being $YY \times yy \rightarrow Yy$. Since all these F_1 individuals were heterozygous in both the genes for tallness and the genes for seed color, the genotypic formula is $Tt\ Yy$.

When the F_1 generation is selfed (that is, pollen from F_1 plants is placed on the stigmas of flowers of F_1 plants) the formula becomes $Tt\ Yy \times Tt\ Yy$. It was pointed out above that a cross between two plants that are heteroxygous for any given gene gives a genotypic ratio of 1 homozygous dominant:2 heterozygous:1 homozygous recessive. At this point it is necessary only to write the symbols for each set of alleles in the problem above, and then to combine the results in order to determine the probable genotype ratios in the offspring of the cross under consideration, because all possible combinations of both of these sets of genes are certain to occur.

$$Tt \times Tt \rightarrow TT{:}2Tt{:}tt$$
$$Yy \times Yy \rightarrow YY{:}2Yy{:}yy$$
$$\overline{TTYY{:}2TtYY{:}ttYY{:}2TTYy{:}4TtYy{:}}$$
$$2ttYy{:}TTyy{:}2Ttyy{:}ttyy$$

Translated into phenotypic terms this ratio becomes the 9:3:3:1 ratio referred to on page 154.

The Growth of Genetics. The twentieth century has seen a rapid expansion in the investigation of problems of heredity. Mendel's experiments were completed and his results announced in 1866 but no one seems to have understood their importance until 1900, the first year of the present century. With the recognition of the significance of these discoveries, numerous investigators began to realize how powerful a tool this new approach could be in clarifying many of the enigmas still remaining in biology. As a result of the many-sided studies which followed, genetics has now become such a complicated science that only the most elementary aspects of the recent developments can be discussed here but some facts necessary in interpreting the phases of botany yet to be introduced may be presented.

Unusual Chromosomes Behavior: NONDISJUNCTION. Chromosomes occasionally deviate from the usual behavior outlined above. When this occurs hereditary behavior also diverges from the standard. As an example, the common jimson weed, a large, coarse, ill-smelling plant of waste ground of almost world wide occurrence, usually has 12 pairs of chromosomes. In some cases, however, one chromosome fails to separate from its mate in meiosis. This type of behavior is known as *nondisjunction*. Such an abnormal reduction division brings about the production of haploid gametophytes, half of which have only 11 chromosomes while the remainder have 13. In other words, one of these chromosomes is in duplicate while all the others are single. If these 13 meet the 12 of a normal gamete, the resulting zygote has 25 chromosomes instead of the usual 24, since one type is represented by three individuals instead of the usual pair. If an 11-chromosome gamete enters into fertilization with a normal one, the resulting 23-chromosome zygote is unable to develop properly. Instead, it dies at some point before reaching maturity.

Since nondisjunction may occur in any one of the 12 pairs of chromosomes there are 12 possible 25-chromosome combinations in the jimson weed and all are well known to those who have investigated them in detail. Each one of these 12 carries its own set of genes and is, therefore, represented by its own phenotypic characteristics such as unusual shapes of fruits, peculiar spines on the fruits, distinctive color patterns on flowers and stems, and other peculiarities.

Only a few species have been studied in sufficient detail to prove that nondisjunction occurs in them, but such action has been found often enough to indicate that it occurs occasionally in many of perhaps all kinds of higher organisms.

In other instances, during meiosis, pieces of chromosomes break loose from their usual locations, becoming attached in reverse, transferring to new positions, or even being incorporated into a chromosome belonging to some other pair. All of these changes bring about new relative positions to each other of the genes and with these new relationships come corresponding phenotypic variations.

These and other pertinent facts that are being discovered have led present-day students of genetics to the conclusion that the genes are not only to be found in the chromosomes but that *each chromosome carries a definite complex of genes peculiar to itself, arranged in a line along its length, with each gene in a definite position.*

POLYPLOIDY. One other type of chromosome modification is known as *polyploidy*. A polyploid plant has more than the ordinary diploid ($2n$) number of chromosome sets and frequently shows such striking vegetative characteristics as greater size, more sturdy development, and greener leaf color when compared with its $2n$ relatives. Polyploidy probably comes about through failure of the reduction division, so that gametes with more than the haploid (n) number of chromosomes are produced. Since these may unite with others of their own kind or with normal gametes, chromosome numbers of $3n$ or $4n$ may be produced in the resulting zygote and in the next generation.

Plants with $3n$ chromosomes are called *triploids*. These are usually sterile. The $4n$ plants, called *tetraploids*, are commonly fully fertile and are frequently more successful than the $2n$ plants from which they are derived. Triploids and tetraploids can be produced in the laboratory by a number of methods. Sudden chilling of flower buds at the time when reduction division is about to take place in anthers and ovules is known to be successful in a considerable number of species and recently certain chemicals have been found to be even more effective (see p. 179).

In nature, triploids, tetraploids, and polyploids with even greater numbers of multiple sets of chromosomes are known to appear from time to time. Those with even numbers of sets, that is, 4 or 6, are commonly fully fertile while those with the odd numbers of 3 or 5 are usually completely or almost completely sterile. The reason for this sterility seems to be the inability of the chromosome sets to separate successfully during meiosis, in this way producing faulty gametophytes and gametes.

MUTATION. A final type of unusual chromosome behavior relates to the genes, themselves. Occasionally a change occurs in one or more of these, causing new phenotypic characters. Investigators have identified alterations in the genes that have brought about new colors in flowers and in grains of corn, differences in amount of chlorophyll in leaves, dwarfness in many plants, and numerous other variations.

Any change that follows Mendelian principles in subsequent crosses is called a *mutation* (*mutare*, to change). There are two general types. Examples of *gene mutations* are given in the preceding paragraph. *Chromosome aberrations* is a term applied to such disarrangements of entire chromosomes or portions of them as occurs in nondisjunction, tetraploidy, or the transfer of parts.

Genes in Action: CHEMICAL ACTIVITY. Whatever else they may be, genes are sources of chemical activity. They cannot be seen by any means as yet devised and yet they influence all organisms in unmistakable ways. The following paragraphs will illustrate a few of these activities.

A cross between two strains of sweet peas, both of which have white flowers, produces offspring all of which have red flowers. If these red-flowered hybrids are selfed their progeny will have a ratio of 9 red to 7 white. At first sight this surprising behavior seems to have no relation to the ratios met previously, but careful analysis by the investigators who first observed this phenomenon has given conclusive evidence that we are dealing here with a usual arrangement of genes, but that they influence one another in a surprising manner.

To clarify the situation it is necessary to recognize the presence of two allelic pairs. The one, which is commonly called C is a basic factor necessary for the production of anthocyanin (see p. 37) although this gene by itself cannot produce that pigment. A second gene, R, likewise, does not cause color to appear. But when both C and R occur in the same individual plant a chemical reaction, not fully understood, takes place in the cells of the petals of its flowers, making red anthocyanin.

In the cross described above, the genotype and phenotype of the two white strains and of their F_1 offspring may be represented by the following symbols:

$$\underset{\text{White}}{CCrr} \times \underset{\text{White}}{ccRR} \rightarrow \underset{\text{Red}}{Cc\,Rr}$$

When the red-flowered hybrid, which is heterozygous for both alleles, is selfed and numerous plants are produced, all possible combinations of the two sets of genes result, producing the 9:7 phenotypic ratio described above.

MULTIPLE EFFECTS OF GENES. A given gene is usually designated by the most obvious effects of its presence. In many cases, however, determiners are known to bring about more than one phenotypic result. For instance, genes controlling the shape of petals of sweet peas also affect the intensity of the scent, and those controlling height affect both the depth of the green color of the foliage and the odor of the flowers. As studies continue to be carried on with the greatest precision, an ever-increasing list of diverse effects of individual genes is coming to light until now it begins to appear that every gene may exert some influence over every other one within the organism.

Applied Genetics. In the corn belt of the upper Mississippi valley placards are often displayed on farm fences announcing the brand of hybrid seed corn that is being grown. Many years of investigation, however, preceded the development of these highly successful strains. During this preliminary period of investigation research workers were using every means at their disposal to interpret the genetic structure of corn. These diverse experiments were carried on primarily for the purpose of discovering the laws of heredity. As a secondary result, professional corn breeders apply this knowledge and raise seed to be sold to farmers. As a consequence, the corn grower can now grow more and better food than he could produce only a few years ago.

Briefly, the methods employed in developing valuable strains of hybrid corn are these: First, ordinary corn of good quality is inbred, great care being taken to see that the pollen from a given plant is placed on the stigmas (called silks) of the same plant. Every precaution is taken to exclude all foreign pollen until self-fertilization has had time to take place. Seedlings from such inbred stock are likely to vary greatly. Many of them are inferior in the extreme; some may not even be able to live while others show only minor signs of degeneracy. A few are likely to be normal.

These normal plants are chosen to be inbred as before and all the others are destroyed. After a few generations of exacting selection all the unsatisfactory and unsuccessful recessives that have been obscured by their dominants are eliminated from the strain. Such pure lines are uniform in quality but produce poor yields. The corn breeder develops several inbred strains at the same time and then hybridizes two of these that may be expected to combine the qualities he wants. When he has found a highly desirable combination he has only to grow large amounts of the desired inbred strains and then cause them to cross-pollinate. The resulting F_1 corn is the hybrid seed sold to the farmer.

In the introduction to the first chapter in this book such hybrid corn is described and contrasted with that which was being grown only a few years ago. The great degree of uniformity that is mentioned results from the fact that both parental strains have been inbred until they are highly homozygous in all their allelic pairs of genes. When two such pure-bred lines are crossed their dominants all appear and both uniformity and vigor result. The F_2 generation is less uniform and less vigorous than the F_1 because Mendelian segregation has taken place and by the third year the farmer usually finds it advisable to buy new hybrid seed.

While corn gives a good example of the economic importance of applying a knowledge of genetics to everyday problems, there is an increasing list of other plants, as well as of animals, that illustrate the principle almost as well. In fact, many of the hybrid vegetable and flower seeds sold by seedsmen owe their superiority to a combination of hybrid vigor and new groupings of desirable characteristics.

Two of the great problems in food production and, in fact, in the growth of plants for any purpose, arise from drought and from the numerous diseases to which most plants are subject. Resistance to these great menaces is to a great extent hereditary. By the application of present knowledge, here and there strains of cultivated plants are being developed that are immune to certain diseases or that are drought-resistant. In these ways,

and in many others, the theories of heredity are being applied to the solution of problems that affect every person either directly or indirectly.

Heredity and Environment. In closing this chapter it is important to recall that the various characteristics of any individual plant are the combined results of an immense number of genes reacting upon each other in such a way that they produce the effects called heredity; and that the environment effectively controls the degree to which these hereditary potentialities can develop.

To illustrate with a single example: If 100 grains of very highly bred seed corn are planted in the best of soil in a season good for growth and are given the best care possible, good results may be expected. If, at the same time, 100 similar grains are planted in poor, sterile soil, and are given no further attention, not more than a meager crop if any at all can result. These two sets of seeds have similar gene combinations and the differences in product come from the fact that even with good heredity, the environment can be so unfavorable as to prevent proper development.

By a change in this experiment it is possible to illustrate the effects of heredity. Some strains of corn produce poor crops even when conditions for growth are good. If 100 grains of this kind of corn are planted in each of the growth conditions described above, the crop on good soil will be poor and that in poor soil will be still worse.

Summary. Genes, the determiners of heredity, are transferred from cell to cell and from generation to generation by way of the chromosomes. By mitotic cell division in the sporophyte, the full diploid set of chromosomes and their genes is supplied to every cell. Meiosis, on the other hand, is responsible for Mendelian segregation, separating the members of the chromosome pairs and distributing them into the various spores. By mitotic division the spores develop the gametophytes and they the gametes. Fertilization—the union of gametes—brings together these assorted chromosomes, forming new pairs in the zygote. The zygote develops into the mature sporophyte.

These recombinations of chromosomes, together with their genes, occur every time fertilization takes place. They are responsible for the 1:2:1 genotypic ratios in the F_1; and the more or less complete dominance exhibited by certain genes changes this into the 3:1 phenotypic ratio.

Occasional mutations occur. These are of several types. Some are *gene mutations* in which the character of one or more genes is changed. Others result from such deviations of chromosome behavior, that is, *chromosome aberrations*, as polyploidy, nondisjunction, and changes in relative position of parts of chromosomes.

SUPPLEMENTARY READINGS

Iltis, "Life of Mendel."
Mendel, "Experiments in Plant-Hybridization."
Reed, "A Short History of Plant Sciences."
Riley, "Introduction to Genetics and Cytogenetics."
Sinnott, Dunn, and Dobzhansky, "Principles of Genetics."

Chapter 11

THE EVOLUTION OF PLANTS

"There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been and are being evolved."

—CHARLES DARWIN

Men often make decisions with their emotions, only to find later that the decisions have not been well founded. The emotions play an important part in human life but they are not useful as a means of discovering facts.

The scientist in his search for truth depends, instead, on such evidences as he can find—all of them—and draws his conclusions on the basis of these findings. The following outline of this chapter lists a few of the evidences which seem to biologists to clarify the question of the source of the multitudes of species of organisms living on earth.

Species. Why are sugar maple trees and red maples so much alike that persons who are not well acquainted with them frequently fail to distinguish between them? And yet why are they so entirely distinct from each other that they fail to hybridize even when they are growing crowded together in a forest?

Questions like these have been subjects for speculation on the part of philosophers for many centuries, and scientists have long tried to find

reliable answers to such problems by means of their observations and experiments. Stated in another way, these persons have studied the meaning of the observed fact that organisms are grouped naturally into rather definite kinds usually called *species*.

The Latin word *species* simply means kind, but in modern biologic literature the term has developed a somewhat more specialized connotation which is easier to illustrate than to define. As examples, silver maple, red maple, sugar maple, and Norway maple are all distinct kinds, or species, of maple trees. Likewise, there are many kinds of elms, cottonwoods, violets, and thistles. This list of illustrations might be extended almost indefinitely, for there are hundreds of thousands of species of plants known. A simple definition of a species as understood by the modern biologist is *a population of individuals incapable of interbreeding successfully under natural conditions with others outside their own group*. In other words, a species is a sexually isolated assemblage of organisms.

Even a superficial comparison of large numbers of plants makes it evident that they fall naturally into small groups of related forms and a more careful study demonstrates the fact that the smaller of these groups combine naturally into larger ones. Order is evident. The question remains as to how species exhibiting such vast ranges of similarities and differences can have originated.

Theories to Account for the Origin of Species. From the dawn of history there have been two views as to how species have come into existence. One of these is the theory of *direct creation*. The other is the theory that plants, and animals also, have changed from generation to generation, in this way producing the various present-day forms. This is the theory of *evolution*. In order to make a fair evaluation of these two concepts it is necessary to understand the exact meaning of both. By comparing these theories with the facts of nature—the evidences—it is possible to discover which is nearer to the truth. This is the method of science.

THE DIRECT CREATION THEORY. The direct creation theory holds that the present species were created, approximately as they now are, at some time in the more or less distant past and that since that time they have changed little or not at all. This concept has been held in a variety of forms during many centuries and by many peoples. In most instances it has been believed that some deity or deities molded earth or other raw materials into the present-day forms of plants and animals. According to this idea no deviation from the original can be great enough to produce a new species, the differences within a species being merely the slight adjustments to environment. The theory of direct creation is well stated by Linnaeus who was a student of this question about two centuries ago. In one of his books he wrote, "There are as many species as there were different forms produced in the beginning by the Infinite Being. These forms, according to the laws of reproduction, have produced more always like themselves." Probably, in the history of human thought, a vast majority of people have considered some variations of this theory to be a satisfactory explanation of the kinds of organisms they have observed. In science, however, majority votes cannot be depended on to establish truth, but the weight of evidence must be taken as the only guide in reaching decisions.

THE THEORY OF EVOLUTION. This theory appears to have originated in human thinking at about the same time as that of direct creation. No one can tell just when either concept came into existence, but both can be found in crude form in very ancient literatures. Some of these date back to periods long before that of the Greek philosophers. It appears that in at least some countries these two interpretations were held side by side by different people in the same communities, much as they are held here at the present.

The theory of evolution has been called by different names at various times, such as "the theory of development" or of "transmutation of species." By whatever name it is called, it holds that organisms are not unchanging; that succeeding generations are not exactly like their parents; and that in a sufficiently long period of time enough change can take place to make new species. *The theory of direct creation is built on the idea of fixity while that of evolution is based on change through the generations.* There are several lines of scientific study that throw light on the question of fixity or changeability,

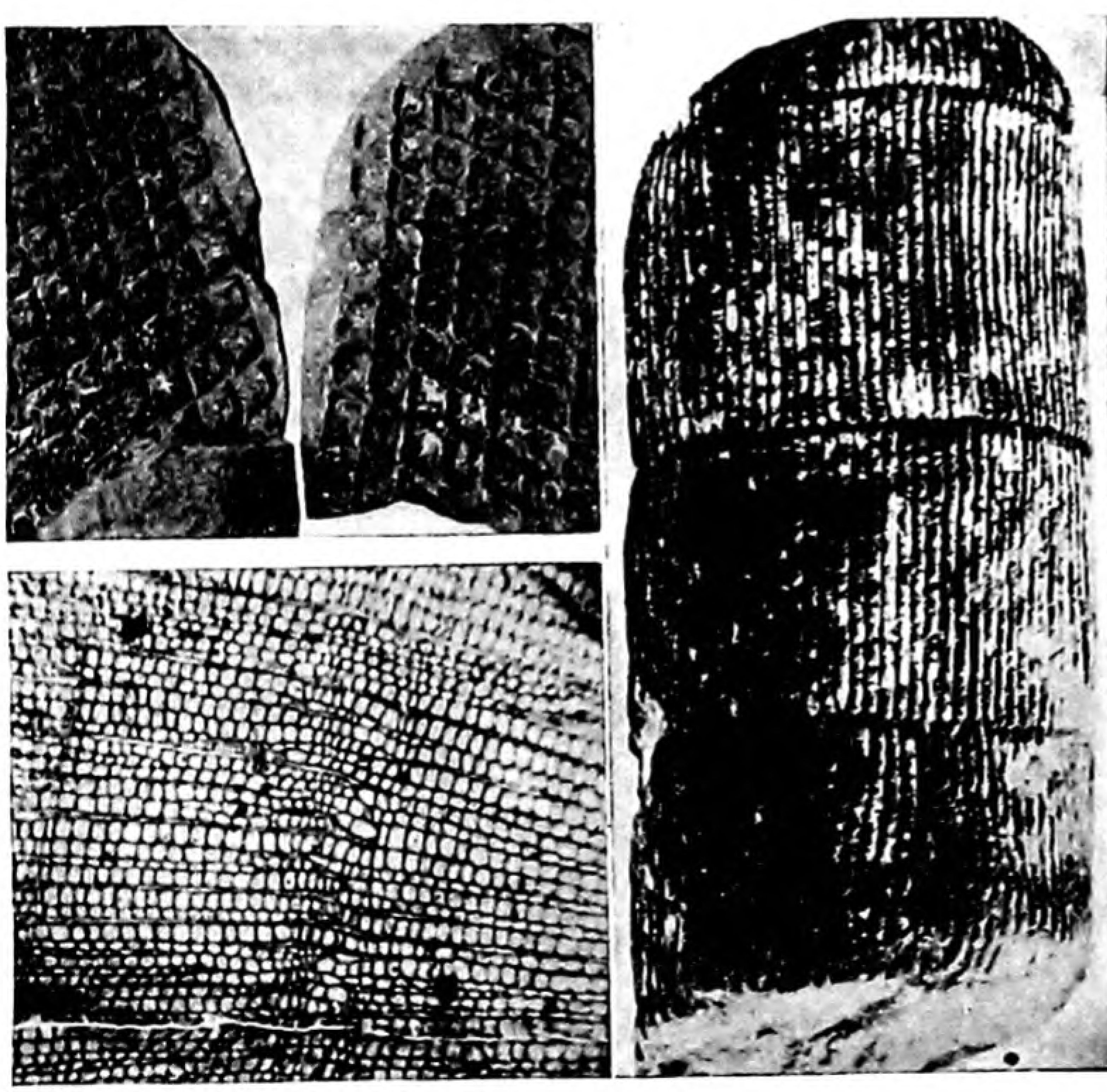
some of the most important of which are geology and paleontology, isolation and the distribution of species, and domestication and classification. Most important of all is present-day investigation.

EVIDENCES FROM GEOLOGY AND PALEONTOLOGY. Geology is the study of the structure and history of the earth; the study of fossils in general is called *paleontology*, and of plant fossils, *paleobotany*. Detailed investigations by many research workers in these fields have established certain points germane to this discussion.

Geologic Processes. Because they are of primary importance in interpreting this evidence, it is necessary to have a clear understanding of erosion and deposition and of the effects of these activities in the preservation of ancient records of living things. When mountain, plateau, and hill are worn down by erosion, a process which is continually going on, materials are largely deposited in lakes and seas. This process is evident in any muddy stream, where soil is being carried from higher to lower levels, toward a body of still water. Along with the deposits of sand and soil in bodies of water, the remains of untold millions of plants and animals gradually sink to the bottom.

Under certain conditions, especially if the water is deep and relatively free from oxygen, or if it contains dissolved materials that act as antiseptics, decay does not take place and these plant and animal bodies are likely to be preserved. In such a mixture of materials from many sources there are almost always considerable amounts of dissolved minerals. Through long periods of time these tend to form rock and thus to preserve in stone authentic records of form and structure.

Plant and animal remains may lie entombed in their rocky covering, or they may be dissolved and carried away or otherwise caused to disappear more or less completely during the long ages of time, leaving only an empty space where they once were. When the tissues are removed in this way and the surrounding matrix remains intact, the surface features of leaves, stems, roots, fruits, and other parts are recorded as *imprints* or *molds*. Occasionally other dissolved materials are deposited in the cavities left vacant in the stone by the disappearance of the plant body, making *casts*. Some of these casts and molds preserve the surface features of the organisms with surprising fidelity of detail, but of course internal structure is not shown.



(*Right*) Cast of trunk of *Calamites* showing nodes and vertical ridges. (*Left, top*) Cast of surface of trunk of *Lepidodendron* showing spirally arranged leaf scars. (*Left, bottom*) Petrification of wood of *Stigmaria*, showing microscopic anatomy including growth rings and other details of wood structure.

Under certain other conditions slow changes occur in which a part or all of the original tissues are gradually turned to stone by *infiltration* of dissolved materials which permeate the entire mass. Changes of organisms into stone by infiltration are called *petrification*. In some cases the actual original substance remains only slightly changed, being supported by infiltrated limestone, chert, or other mineral. Petrified tissues are sometimes so perfectly preserved that even cell structures are clearly visible when thin sections are examined with the microscope.

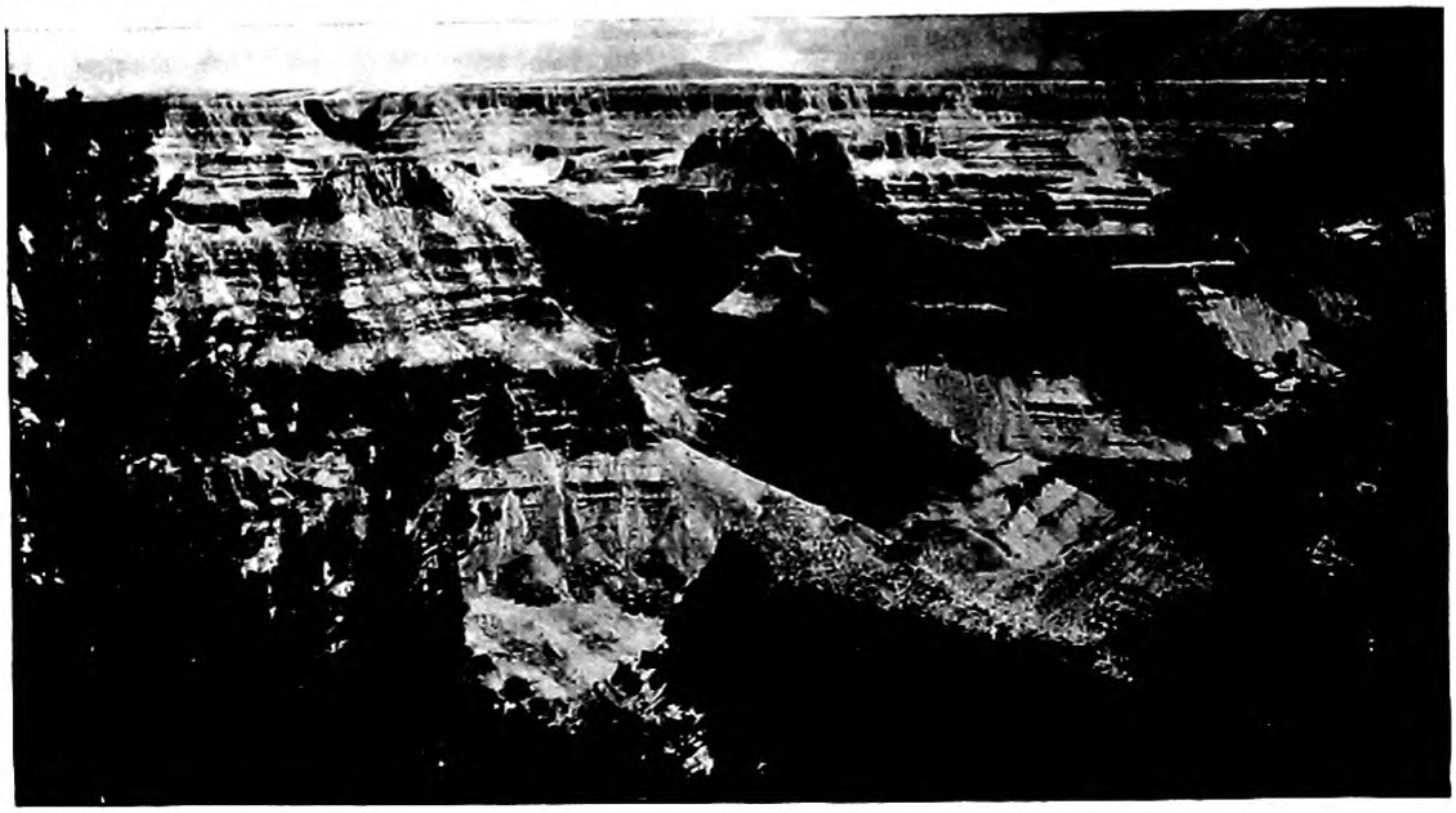
Other more or less perfect records are sometimes found where plants have been covered with volcanic ash, have lodged in peat bogs, or have become buried deep in the mud of deltas. With this kind of protection, organisms of decay have little opportunity to grow, and many objects are well preserved with relatively little change for many thousands of years. Even pollen grains that have been buried deep in masses of peat since the Ice Age can be identified with great certainty, so perfect is their preservation.

Fossils. Any evidence of life that existed in ancient times is a *fossil.* Because of the directness of the evidence given by fossils, they are of special value in answering questions concerning fixity or changeability of plants through the ages.

Although fossils give clear answers to many questions of plant relationships, the records are incomplete and at times difficult to interpret. An understanding of the conditions under which they form makes the reason clear. The vast majority of organisms disintegrate promptly after they die and leave no recognizable trace of themselves. Only the relatively few plants and animals that are covered by water or are in some other way protected from bacterial action can fossilize. Because decay prevents fossilization, delicate forms are much less likely to leave records of themselves than woody or otherwise resistant ones. This fact probably explains why only a few algae are preserved, with the exception of those that have compounds of lime or silica in their cell walls, and that not many liverworts or mosses have been found.

One other very important reason why the record is known incompletely is that fossils are distributed over almost the entire surface of the earth, and in many places are buried in rock strata thousands of feet deep. Therefore, it is only in the rather limited locations where man disturbs the earth's crust, as in mines or road cuts, or in those places where erosion or other processes of nature lay bare the ancient deposits, that these specimens become available for study.

The Fossil Record. Although many kinds of fossils probably have not yet been discovered, the order in which known forms were deposited and their relative ages are fairly accurately known. Common observation proves that sediment laid down in any body of water takes the form of layers deposited one on top of the other in an orderly manner and it is quite possible to determine which layers are more recent even after ancient deposits of this kind have been hardened into stone. In mines and excavations and in almost any place where erosion



Grand Canyon, showing horizontal layers of rocks. In these layers are to be found a succession of fossils that were formed during hundreds of millions of years of time. Photograph by Josef Muench.

cuts through stratified rock, the geologist can find fossils. Many of these are limited to rather restricted periods of time in the development of the earth and are, therefore, markers that indicate the age of all deposits in which they occur.

One of the most extensive of these openings in the earth's crust is the Grand Canyon in Arizona where the Colorado River has cut a channel 280 miles long and more than a mile deep in the deepest part. This channel is eroded through the rocks that form the high plateau of the region. Here, for thousands of feet, the strata reveal the history of that region to the eye of the understanding student of geology. The highest part of the rim of the chasm is of rock that was laid down in the Pennsylvanian period (see geologic table, p. 154), and the river has now cut down to such a depth that it is flowing over ancient granites and related rocks that crystallized out of molten materials when the earth was relatively young.

The walls of this canyon contain a record of living things and of the conditions in which they existed in an almost continuous story covering a period hundreds of millions of years in extent. Ocean bottoms are preserved there, and desert sand dunes, and faults in which the strata broke and slipped, probably resulting in ancient earthquakes. Likewise, there are fossils of many kinds, all distributed in a most orderly manner. When the story told by these rocks and their embedded remains of ancient plants and animals is pieced together with those from other places over the world, a most enlightening panorama of earth history emerges.

Geologic investigations have proved that during earth history there have been many upheavals and subsidences in the earth's crust, producing plateaus and mountains on the one hand and ocean basins on the other; forming continents, parts of continents, or islands here and submerging other bodies of land there. By this means, parts of the ancient ocean bottoms or of swamps are now elevated into plains or even high mountains. As a result of this kind of action, one may now find in the Rocky Mountains fossil shells, the bones of sea animals, and plant remains in great quantities, all imbedded in stone high on mountains thousands of feet above the ocean. Great beds of shells of ancient oysters and of corals more than a mile above sea level are mute but convincing proof that this land was once the ocean bed.

The production of fossils has been in progress for extremely long periods of time. Various estimates have been made from many kinds of evidence. Using the most accurate data known, calculations of the age of the earliest indications of life place that age at perhaps 1 billion or more years. It is true that this is only an estimate, but it is certain that life has been here for eons of time. Even one without geologic training cannot fail to be impressed by the immensity of the time required to lay down as sediment the layer after layer of rocks that make up the strata of a Grand Canyon. Even so, according to the geologist, the depth of this great canyon represents only a small fraction of the total thickness of the stratified portion of the earth's crust. Then, recognizing the fact that many of the simplest plants could rarely if ever fossilize because of their extremely delicate structure, it is apparent that life may have been present on earth long periods of time before the formation of the oldest fossil that has been found.

Fossil Plant Sequence. The paleontologist finds that when the strata are arranged in order of age, the fossils relate an enlightening story (p. 169). The most ancient plants that have been found are extremely simple. They belong to the Proterozoic Era. A few are thought to be bacteria and all the rest seem to be properly classified as extremely primitive algae, somewhat similar to certain present-day forms that secrete lime in their cell walls. Relatively small numbers of these fossils have been discovered.

The rocks next younger, belonging to early Paleozoic times, appear to have been deposited in oceans, for primitive sea animals are abundantly represented, although plant remains are not numerous. Obviously, there must have been chlorophyll-bearing aquatic plants in large numbers furnishing food and oxygen for the swarms of simple animals. Of the fossil plants that have been discovered, almost all seem to be of algae, although the structure of a few shows that they probably grew on land. The total vegetation of the earth by the end of the Silurian period, perhaps 355 million years ago, ap-

Devonian landscape showing forest made up of large but primitive members of the Cycadofilicales, Sphenopsida, and Lycopsida. The small undergrowth includes members of the Psilopsida. (From mural by Charles R. Knight in Chicago Natural History Museum.)

pears to have been mostly algae floating in water and growing on wet soil, with a few higher forms creeping out onto dryer land.

Although they were neither striking in appearance nor numerous, these first land plants were very important in the history of vegetation. They are called the Psilopsida and are described in more detail in Chapter 18. They had neither roots nor well-organized leaves, but never before in all time had there been plants with wood and conductive tubes, capable of living with their upper parts in air and with rhizomelike structures absorbing water from the moist soil. But with all these advances out of water and into air there were no trees, nor grass, nor flowers. Such is the picture the fossils reveal.

The Silurian period extended over some millions of years and ended in a time of great change in the earth's crust. During Devonian times, which followed immediately, mountains arose and much more of the land moved upward out of the water. Under these changing conditions it must have been necessary for plants either to change or to die. Doubtless many did die. But the fossils indicate that many types developed.

These changes in plant environment and form came relatively rapidly. Trees and shrubs appeared. They were far more primitive than present-day species, it is true, but they were also greatly advanced beyond Psilopsida. During this period, spores became much more common, still further adjusting these plants to aerial surroundings. At last some of the vegetation was fully established out of water.

By the end of the Devonian period there were numerous ferns or fernlike plants many of which had seeds. Imagine the amazement of the botanist who first found a fossil seed belonging to an ancient fernlike leaf! Nevertheless, if we could return to Devonian times we should begin to feel much more at home than in the earlier periods of earth history, though our senses would still miss much that we now experience. A sentence from the book, "Plant Life Through the Ages," by Seward, an English paleobotanist, is a striking summary of those things we should miss from our customary environment. He says, "Neither in the peat nor in the pools should we see any flowers: a sheet of uniform green relieved by the brown tints of dead or decaying herbage: no cries of birds, nor sounds other than those made by fitful breezes or violent storms."

Toward the end of the Paleozoic era, forests of trees and patches of undergrowth became extensive. Some of the trees were gigantic horsetails much like the small ones of the present time while others were equally large club mosses a few of which had seeds; and still others were ferns, some of which were superficially like modern ones. Certain of these had much of the appearance of the tree ferns of the present-day tropics. A good many of these fernlike forms bore seeds. They are sometimes called *Cycadofilicales* from their combined cycad and fern char-

acteristics, and sometimes *Pteridosperms* (*pteridos*, fern; *sperma*, seed). The luxuriance of the vegetation became very striking. The plants of those times seem to have belonged to orders but not to families, genera, and species that occur now.

Progressing through Mesozoic and Cenozoic times, plant life continues more and more strongly to suggest modern types. Yet, it is only in the more recent strata that the present-day botanist would begin to feel really at home in the fossil landscape, and up to the very last he would fail to find the most advanced types. In this way the story unfolds until the present is reached.

GEOLOGIC RECORD*

Era	*Period, and greatest number of years back from the present*	*Characteristic plants*
Cenozoic	Quaternary 1,500,000	Modern conifers and flowering plants.
	Tertiary 60,000,000	Primitive modern species of seed plants associated with species that are now extinct.
Mesozoic	Cretaceous 120,000,000	Many flowering plants; genera but not species are modern.
	Jurassic 150,000,000	Primitive angiosperms, conifers, ferns, and cycads.
	Triassic 180,000,000	Primitive cycads and conifers; no angiosperms.
Paleozoic†	Permian Pennsylvanian Mississippian 300,000,000	Great forests of Lycopsida, Sphenopsida, Filicineae, and fernlike seed plants.
	Devonian 345,000,000	First seed plants; first Lycopsida, Sphenopsida, and Filicineae.
	Silurian Ordovican 540,000,000	Marine algae; a few emerging from water; the first stele, in Psilopsida.
Proterozoic	1,000,000,000	Bacteria and algae only; these presumably blue-green; poorly preserved.

Read up from bottom

* Adapted largely from DARRAH, "Textbook of Paleobotany."

† Pennsylvanian and Mississippian together are often called Carboniferous

From the facts presented above it is evident that the more ancient rocks contain the simpler fossil forms and none of the higher, more complex species; that gradually the more highly organized groups appear in the newer rocks; and that even the earlier types are replaced by somewhat different, but closely related kinds. Thus modern organisms slowly appeared. The accompanying table will summarize these points.

EVIDENCES FROM ISOLATION AND THE DISTRIBUTION OF SPECIES. Somewhat more than 500 miles west of the coast of Equador there lies on the equator a group of islands, the Galapagos Archipelago. These islands are of volcanic origin, having arisen by upheaval from the bottom of the Pacific. Exacting studies of the species living there a century ago, before man began to interfere, have shown that the plant and animal population was much like that of the equatorial coast of the South American continent. On the other hand, little relationship was evident with the flora and fauna of distant parts of the world having a similar climate. Even the species on the various ones of these islands separated by considerable expanses of the sea were found to be somewhat distinct, but closely related to each other.

In a situation such as this, it would hardly be possible to explain distribution on the basis of differences in either soil or climate. Obviously, some other factor is at work. If this were an isolated example it might be dismissed as a coincidence, but further explorations of isolated places show it to be a rather general situation. In fact, it is so general that extensive observations of the distribution of animal species led Jordon and Kellogg in their book, "Evolution and Animal Life," to say, "Distinctness is in direct proportion to isolation." This statement seems to apply as well to plants as to animals.

Isolation results from barriers. Almost all species of plants migrate to some degree, but barriers limit the direction and rate. Barriers to water plants may be land; to marine plants, fresh water; to desert plants, bodies of water; to plants of humid regions, deserts or high mountains; to plants on mountains, deep valleys; to those of polar regions, a warm climate; and to plants of the tropics, frost.

EVIDENCES FROM ENDEMICS. Species of very limited distribution, such as those mentioned above, are called endemics. Hundreds of endemic plants and animals are known. They are most common where a relatively small number of individuals is effectively cut off from the main body of their relatives. Large numbers of examples can be found on the tops of mountains that have deep valleys around them, on oceanic islands, and in other small isolated places. Such physical barriers as these bring about *geographic isolation*. After a considerable period of time, differences of the isolated group often become so great that, when compared with the plants most like them, they cannot be included in the main body of the species, while at the same time they retain sufficient similarity with that group definitely to indicate close relationship. A critical study of large numbers of instances convinces biologists that the development of new forms in isolated areas results from the combining in the offspring of the segregated individuals of those peculiar gene combinations which the segregated parent stock happened to have, or that have come about as a result of changes within the chromosomes and the resulting mutations. No two individuals are exactly alike, and barriers that prevent crossing with the main body of the species isolate and intensify, that is, make homozygous, those hereditary peculiarities that the segregated individuals possess. In this way, in a relatively few generations in isolation, new types arise, and the longer the period of time and the more completely segregated they are the greater the degree of distinctness that develops between the two groups.

In addition to geographic isolation there is another type that is now coming to be recognized. This is *genetic isolation*. As shown in Chapter 10, various kinds of gene changes occasionally occur (p. 145). Sometimes they are of such a nature that they prevent the formation of fertile crosses with the parent stock, sometimes they bring about considerable shifts in flowering time in the new plant, or they may fit it for growth in a somewhat different type of environment. An example of the last type of behavior is found in two very closely related wild pinks. These are capable of making fertile crosses but do so only infrequently because they commonly grow in diverse soils and therefore seldom live near to one another.

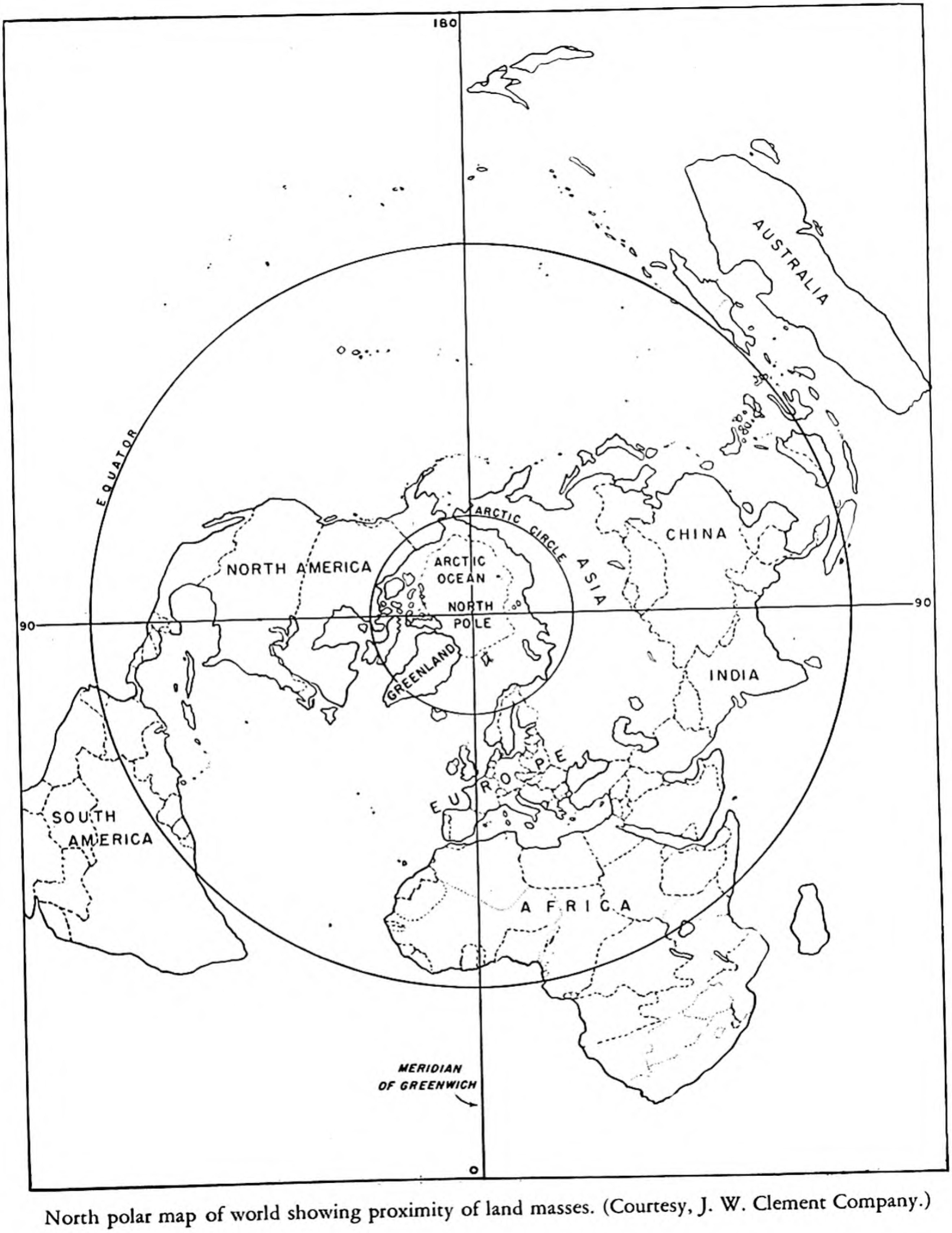
While these genetic barriers are less easily recognized than those of a geographic nature, they are sometimes quite as effective. For this reason, local endemics appear occasionally in large populations, and if their hereditary characteristics make them as well adjusted to their environment as the stock from which they arise they are likely to spread gradually into new territory. At times, especially in the case of polyploids, they are definitely more sturdy than the parent species. Under these conditions the mutant may be expected eventually to replace the ancestral stock in ever widening areas.

EVIDENCES FROM COSMOPOLITAN SPECIES. In places where physical barriers are very slight there are likely to be many species of very wide range. These are called *cosmopolitan species*. A glance at the map of the world (p. 156) shows that the barriers to land plants between North America and Eurasia are not great because these continents are almost connected by land bridges, especially between Alaska and Siberia; that the distances are gradually greater and therefore more nearly completely impassable to spores, seeds, and other means of propagation, between these continents as they extend southward; and that water is more expansive and land less extended in the Southern Hemisphere, with great distances between the continents.

A comparison of the flora of these different parts of the earth shows significant features. The plant life of the Arctic regions is remarkably uniform. Many of the same species of willows, birches, mosses, lichens, algae, and numerous other plants extend entirely around the North Pole. Indeed, the majority of successful species in the north polar regions are extremely cosmopolitan, with only occasional local endemic races that seem to be of the genetic type.

The next band around the earth, which constitutes the North Temperate Zone, is occupied by many of the same genera and much of the same type of plant life on the various continents, but there are comparatively few identical species, even in practically the same climates.

On the continents that are crossed by the Tropics and the South Temperate Zone, one finds very



North polar map of world showing proximity of land masses. (Courtesy, J. W. Clement Company.)

wide differences even in the families of plants. Referring again to the map of the earth, it is evident that plant distribution agrees well with the statement quoted above from Jordan and Kellogg: "Distinctness is in direct proportion to isolation."

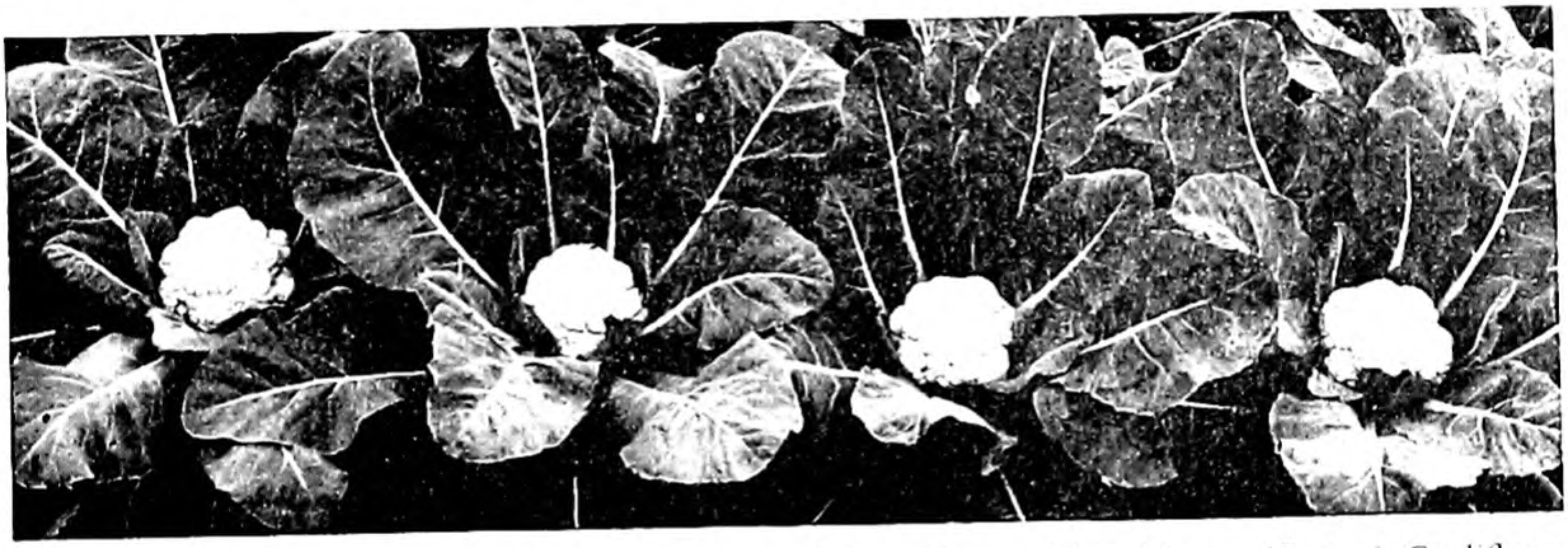
The question is often raised as to whether these different species may not be merely well placed to agree with dissimilar climatic conditions on the various continents. The plants themselves can answer this question. Within historic times man has carried many kinds from their native homes to distant lands across many barriers. Cacti of the American deserts have been transplanted into the corresponding climatic regions of Africa, Australia, and southern Europe, becoming in some places such a nuisance as to be bad weeds. Yet cactus is indigenous only to the Americas. In many of their new homes these plants have become so thoroughly established that those who are not botanists have no idea but that they are a part of the native vegetation.

Such illustrations could be multiplied almost indefinitely. Many of the most persistent weeds in North America are indigenous to other parts of the earth and have been introduced here since modern means of transportation have permitted them to come in. Russian thistle, *Salsola kali*, a European weed, is a good example. It was brought into South Dakota in 1874. It is now distributed extensively as a very successful weed over wide areas of the United States and Canada. Numerous other examples could be cited, illustrating the same sort of success of other plants that thrive as well, and often better, when introduced into parts of the earth far from their place of origin. Such situations show conclusively that the native home of a given species is not necessarily the best place for its growth.

EVIDENCES FROM DOMESTICATION. That man changes his plants and animals almost at will is so well known, especially to those who live on farms, that the fact needs only to be mentioned. The good corn farmer chooses his seed with the utmost care, thus producing a crop with suitable size of ear, number of rows of grains per ear, satisfactory shape and size of grain, and other characteristics to suit his need. In many communities of the corn belt there are farmers who specialize in the production of high standard grain to be sold for seed. To a greater extent each seedsman develops his own special strains of vegetables and flowers that are somewhat different from those produced by others. Man changes his plants rapidly and with relative ease when he chooses to do so.

There can be little question that cultivated plants have been derived from wild species by human selection through the centuries. Man has in the past, as at present, chosen as parents for his crops those individuals that met his fancy. So well has he succeeded in changing and improving them that it is now difficult or even impossible to be certain of the ancestry of many of them. Wild forms of apples, strawberries, blackberries, wheat, and many other

Wild cabbage, *Brassica oleracea*. (Photograph taken at Cardiff, Wales. Courtesy, the late Professor C. J. Chamberlain.)



Cultivated derivatives of wild cabbage. (*Top, left*) Kale. (*Top, right*) Cabbage. (*Bottom*) Cauliflower. (Courtesy, W. Atlee Burpee Company.)

cultivated crops are known, but they are far inferior to the cultivated fruits and crops that have been developed from them.

An excellent example of a group of vegetables whose ancestry is definitely known is that of cabbage and its relatives. To this day, on cliffs along the sea coasts of western and southern Europe there grows a coarse weed, the wild cabbage, *Brassica oleracea*. It is much like the kale found on vegetable markets in the United States. In fact, kale seems to be only the slightly changed wild plant, which has been introduced as a product of garden and farm in many parts of the world. Neither the wild cabbage nor cultivated kale produces heads, although the upper leaves of the latter tend to become grouped into tender, edible rosettes, suggesting the possibility of head formation.

Brussels sprouts deviates from the wild form by developing into small heads the lateral buds on the main stalk. In like manner, in the head-forming cabbages, the terminal bud becomes first a rosette somewhat like that of kale and then continues to produce in-curled leaves until the head takes shape. Cauliflower grows a fleshy flower cluster in which the flowers are usually nonfunctional. All these diverse kinds and several others appear to have been developed by human selection. Plants with desirable variations were chosen in earlier times for the production of the seeds from which to grow the crops. These changes from wild cabbage seem to have been just beginning at the dawn of human history. Today seedsmen use this same method to produce whatever shape or color of head the trade demands.

EVIDENCES FROM CLASSIFICATION. In the next chapter it is pointed out that numerous attempts have been made to find a workable classification of plants, and that the older groupings were found to

be unsatisfactory for a variety of reasons. The theory of evolution recognizes close relationships between those organisms that are alike in most respects, and more remote kinship between those that are dissimilar in many characters.

Most of the comprehensive classifications of recent times have resulted from attempts to express the degrees of actual kinship or, in other words, to recognize the similarities and dissimilarities of the gene combinations that have come down to these various groups from their ancestors. That is, investigators in the field of classification have made efforts to place in each group, whether species, genus, family, order, class, or division, those plants which are more closely related to one another than they are to the plants of other groups.

It is to be expected that opinions will continue to differ in the future as in the past about many details of such classifications and that groupings will have to be changed from time to time as new facts are discovered and new relationships become evident. It should be clear, however, that the only organizations of the plant kingdom yet found to be really satisfactory are based on evolutionary concepts. While this observation in no sense proves that the theory of evolution is a fact, it does not contradict it.

Chemistry and Kinship. Like searchers examining a gigantic unknown cave, scientists frequently meet with surprises. Sometimes the paths they follow lead them into dead ends in which further progress is impossible. At other times their discoveries open to them great rooms, which, when scrutinized, are found to have many corridors leading into still different unexplored places. The great divisions of science are like these rooms and the scientific investigators are the explorers, each making discoveries within a single compartment. Every room is more or less distinct from the rest, but when examined in detail all are found to have outreaches into all the others.

With the development of knowledge in the numerous phases of botany, zoology, chemistry, physics, and geology it is becoming more and more clear that the field of science is not a group of unrelated subjects, but is a single unit which has been divided, for convenience, into several more or less separate but artificial parts.

This course is an exploring tour of one of these sections of science, called botany, and, at the moment an important segment, which has been named classification is being examined. Unexpectedly it is discovered that in dealing with plants it is also necessary to work with animals and with chemistry. Since *bios*, the Greek word for life, refers to all kinds of living things and their activities, this phase of science is called *biochemistry*. Without naming it at the time, the earlier discussions of enzymes, hormones, genes and numerous related topics were more or less within the field of biochemistry.

From time to time throughout this book, it has been stated that the effects of the genes in the development of the individual are almost certainly in part, or perhaps entirely, brought about by their control of the chemical reactions within the protoplasm. In addition, in Chapter 10, it was stressed that differences in gene complexes are responsible for the hereditary distinctions between diverse individuals. It is now becoming obvious that the divergences between groups as well as individuals are fundamentally chemical and that these distinctions are under the control of the genes.

While these concepts, based on combined studies of genetics, details of chromosome structure, and biochemistry have been growing, biologists have developed means of measuring degrees of chemical relationship between living things. A considerable number of years ago a method was discovered by which to identify the blood of various kinds of animals. Later the same principle was applied to studies of the sap pressed from the tissues of plants. The exact methods are not important in this course but the underlying principle can be made clear.

In Chapter 5 the structure of proteins was described briefly. It will be recalled that the molecules of amino acids unite in various combinations, each forming a characteristic super-molecule of a particular protein, and that immense numbers of these groupings can occur. Some years ago it was discovered that a laboratory animal, such as a rabbit or guinea pig, reacts to any protein from a source outside its body in the same way that it does to invading disease germs. In other words, the animal

becomes "immune" to the foreign protein. This immunizing action is brought about by means of a kind of vaccination in which repeated doses of the protein are introduced into the circulatory system of the laboratory animal. Thus, if repeated injections of the sap from a lily plant are introduced under the skin, the animal becomes immune to the proteins peculiar to the lily much as it would be immunized to the bacteria that cause typhoid fever if a typhoid vaccine were used.

Additional experiments-have shown that when a small amount of the sap from a lily plant is mixed with the clear serum taken from the blood of a lily-immune animal the serum soon becomes milky in appearance. If, on the other hand, the sap of a near relative of the lily, such as that of amaryllis or iris, is mixed with lily-immune serum, a similar, but somewhat less intense change in appearance occurs. When the investigation is carried still farther and plants far different from the lily, such as ferns or moss are used, the change occurs slowly and is slight in amount. In other words, a fair measure of the degree of chemical similarity and apparently of biologic relationship between any two species can be established by this method.

By using as immunizing agencies the sap of plants belonging to hundreds of species, it has been possible to measure degrees of relationship between them and large numbers of others.

Comparisons of these results with the usual classifications which are based chiefly on structure and methods of reproduction, show a remarkable agreement between the two. In fact, each seems to supplement and correct the other, and as a result it is becoming more certain that present ideas of classification are based on fundamental facts.

Not only do these newer discoveries in the field of biochemistry point the way to the causes of variation among organisms, but they as definitely demonstrate that the various kinds of organisms, whether they are pond scums or mosses or oak trees, or even members of the animal kingdom, are remarkably similar in many fundamental ways. As examples, throughout the living world, plants and animals carry out steps in the processes of respiration by means of combinations of identical or practically identical chemical substances. Likewise, it is becoming evident that many of the vitamins produced by plants are important in their metabolism. When these plants are eaten their vitamins bring about these same necessary activities in the protoplasm of the animals.

From rapidly increasing evidence it seems certain that living things are all fundamentally related to each other because they have received certain basic characteristics by inheritance down through the generations from ancient ancestors. Interpreted in this way the variations between individuals and groups have probably arisen from larger or smaller chemical changes within the genetic system of the protoplasm.

These lines of evidence and a great many others less easily followed by persons without highly technical training, have combined to convince modern biologists that evolution is, and has been, continually taking place. Nevertheless, in any field of science, the ultimate goal of investigation is not merely the discovery of the processes occurring in nature, but also the manner in which these activities occur. The following pages will outline some of the results of investigations into the way evolutionary changes come about.

The Mechanisms of Evolution. To the scientist actively dealing with the evidences, *evolution means heritable change of living things as generation succeeds generation.* When, with increasing information, the evidences became so numerous and conclusive that scientists were convinced of the truth of evolution, there remained the problem of the causes and methods which bring it about. From the early days of modern science investigators have attacked various phases of this problem and gradually the solution seems to be taking form.

It has become increasingly clear that the changes referred to as evolution must depend upon the variations that are inherited, and most of the attempted explanations have hinged upon the different theories of the causes of variations. Some of the older of these theories have now been discarded and are almost wholly of historic interest. Here it is necessary only to deal with those that definitely help in explaining evolution as understood by modern biologists. The remainder of this chapter elucidates the modern point of view.

CHARLES DARWIN'S EXPLANATION. Charles Darwin was one of the most important contributors to an understanding of the question of species. Unfortunately he and his ideas have been greatly misunderstood and sometimes badly misrepresented. Because of his importance in this connection, his method of work and his theory should be understood thoroughly.

Charles Darwin began the study of medicine during his young manhood, and then changed his course and completed his preparation for the ministry. During his childhood and extending throughout his student days he was a careful observer of natural phenomena. While at Cambridge, preparing for a life of ecclesiastical duties, he made frequent excursions into the fields and along the sea in company with a young scientist named Henslow. Henslow was much impressed with Darwin's ability to make discoveries and interpretations of scientific importance.

In those days Great Britain sent out considerable numbers of exploring parties, some of which took extended voyages. It was customary on these voyages to take along a young but promising naturalist to collect specimens of many kinds and to make such studies of his findings as might be possible. On one such occasion Her Majesty's ship, *The Beagle*, carried its crew of officers and seamen, and through the good offices of Henslow, Darwin, then 22 years old, was the official naturalist.

This five-year trip from 1831–1836 was the turning point in his life, and he returned from it a scientific investigator. He began the voyage a thorough adherent of the theory of direct creation, accepting the usual ideas of his time, but the facts he observed forced him to question this hypothesis. Within a few years following his return from this journey he collected great masses of evidence from numerous sources in an attempt to satisfy his mind on the subject. Finally he confided in a letter to a friend: "I was so struck with the distribution of the Galapagos organisms, etc., etc., that I determined to collect blindly every sort of fact which could bear in any way on what are species. I have read heaps of agricultural and horticultural books, and have never ceased collecting facts. At last gleams of light have come. and I am almost convinced (quite contrary to the opinion I started with) that species are not (it is like confessing a murder) immutable."

When Darwin became convinced that species are not fixed but that living things slowly change from generation to generation, his next great task was to try to determine how such variation might take place. In this attempt he collected vast amounts of information from which he drew his conclusions. His results were published in his "The Origin of the Species" in 1859. The observations on which he based his theory were, (1) variation, (2) domestication, (3) overproduction, and (4) the struggle for existence. Out of these observed facts he drew the conclusion that natural selection is a normal result. A brief discussion of each of these points with a few illustrations will be sufficient to make clear his line of reasoning.

VARIATION. It is necessary only to mention the fact that no two individuals, plant or animal, are exactly alike, even those having the same parentage. Just as it is easy to distinguish acquaintances because they are sufficiently different from each other, so those who know plants and lower animals intimately are able to see as great differences in them. The student can readily test this statement for himself. Someone has said that "variation is the most invariable fact in the universe." Darwin was much disturbed because he knew of no cause for variations. It is known now that there are two types of causes, heredity and the conditions under which the plant grows, that is, environment. To illustrate the difference between the effects of heredity and environment it is necessary only to call attention to the fact that a plant may be dwarf because it inherits dwarfness from its ancestors or it may be stunted by disease or from lack of water, light, or suitable soil. Which of these, heredity or environment, would permanently affect its descendents? In answering this question, it should be remembered that heredity is controlled by the genes.

DOMESTICATION AND ARTIFICIAL SELECTION. To those who deal with domestic plants and animals it is obvious that man changes them continually to suit his desires by simply choosing for propagation those individuals that vary in desirable direc-

tions. If such changes could not be brought about, floriculture, agriculture, and horticulture could be carried on with only slight success. Darwin reasoned that since man could in a few years bring about such marked changes in his plants and animals as were to be found everywhere, possibly natural processes could accomplish as much in the long ages of time.

OVERPRODUCTION. "There is no exception to the rule that every organic being naturally increases at so high a rate that if not destroyed, the earth would soon be covered by the progeny of a single pair." If this quotation from Darwin seems improbable, let the student choose for study any plant in nature and reach his own conclusions. Few plants average as few as ten seeds or other propagules per year, and many produce thousands. Taking ten as a conservative figure, how many offspring would an annual have at the end of ten years? But this is the rate of increase of only one individual, and it may be assumed that the other members of the species are each reproducing at the same rate, and that there are hundreds and thousands of other species scattered over the earth behaving in a similar manner. What must become of all these potential plants that do not appear in the population? Often not 1 per cent of the seeds produced grow into mature individuals that, themselves, produce seeds.

THE STRUGGLE FOR EXISTENCE. Overproduction results in a struggle for existence. Darwin's reference to struggle is unfortunate because there is no reason to suppose that plants actively strive with one another. Rather, they grow if opportunity offers and the growth of some is certain to interfere with that of their neighbors. Interpreted in this way, the reality that Darwin observed remains. Growth, maturity, and reproduction usually ensue unless the plant starves, dries up, or is destroyed by disease or animals.

NATURAL SELECTION. The foregoing premises are facts that anyone can observe. The only theoretical part of this argument is Darwin's conclusion—that on the average those individuals that vary in favorable directions are more likely to live and leave offspring than those that vary in less valuable ways, thus passing on to future generations the best characteristics.

Summarizing in a little different order, attention is called to the facts that man by selection makes great changes in his plants and animals; that many more individuals are produced in nature than can possibly find food and other necessities of life; that, therefore, far more die than survive; and that no two individuals are exactly alike. Darwin's theory holds, then, that under these conditions it is to be expected that those individuals best adjusted to their surroundings are likely to be the ones that will survive and leave offspring, transmitting to their descendents those characteristics that have made them successful. Thus, generation after generation, gradual improvement occurs.

It is easy to illustrate this theory with such plants as those of a weed patch. Myriads of seeds of many kinds find lodgment in the area every year. Some may be entirely unable even to germinate. These die. Others may begin their growth but require more water and light than are available. They dry up, or starve. Certain others may be successful weeds but of these there are likely to be many more than can possibly survive in the limitations of this space. There results a struggle for existence. But some are better prepared to live than are others and, on the average, the better adapted individuals will survive and leave offspring with the weedy characters still more highly developed. In this way natural selection has occurred, better fitting each generation to its conditions of growth. Thus to Darwin's mind, natural selection, that is, the elimination of those not well fitted for their environment, largely accounts for both the development of individuals better able to cope with conditions, and the fine adaptations of plants to their surroundings.

MENDEL'S CONTRIBUTION. Charles Darwin referred to variation as one of the foundations of his theory. At the same time he often said that the causes of variations were quite unknown and must be explored before a complete answer to the species question could be had. At the very time these statements were being published, Mendel was quietly at work on this same problem in the little monastery garden at Brünn. Mendel's laws of heredity have been discussed in Chapter 10.

While Mendel primarily studied heredity, his discoveries, and those of later investigators who

profited by his work, have come to hold a necessary place in modern explanations of evolution. Obviously, evolution could not occur except by means of hereditary variations. A knowledge of Mendelian ratios has provided a basic understanding of them.

The solution of almost any problem in science leaves, as a residue, other unsolved questions, the gradual answering of which constitutes the growth of science. In this case the discovery of Mendel's laws left unexplained the immediate question of the sources of the variations which are inherited in later generations. The next section deals with this question.

DE VRIES AND MUTATIONS. At the very close of the nineteenth century a solution to the problem of the origin of variations began to be reached by Hugo de Vries, a Dutch botanist. While studying in a deserted garden plot he found that in a patch of evening primroses, *Oenothera lamarckiana*, there were some plants of apparently the same stock which were quite different from the rest. He removed these to the botanical garden where they could be closely observed, and began keeping a careful pedigree of the offspring of each individual. In succeeding years he kept a record of thousands of plants, applying methods similar to those used with thoroughbred animals. A dozen or more new forms appeared among the seedlings he raised. Many of these were so distinct from their parents as to have been considered new species if their ancestry had not been known. Most of the new strains have bred true in subsequent generations, and the parent stock, year after year, continues to produce numerous individuals of these new forms.

The sudden appearance in plants or animals of new characteristics that persist and Mendelize generation after generation, is called *mutation* and the new type is called a *mutation* or a *mutant*. Later observations show that this kind of behavior is not limited to *Oenothera* but many plants and animals produce occasional mutants. Some of the new forms are well fitted to survive while many others would not persist without human protection.

As a result of these discoveries, de Vries developed the theory that evolution takes place through the action of natural selection on mutants. His theory is based on Darwin's ideas, departing from them in only one respect. Darwin made no distinction between hereditary characters and those which fluctuate because of differing growth conditions, while de Vries' concept holds that mutations produce the effective variations on which natural selection acts.

Some of the variations that Darwin studied were probably mutations, while others may have been Mendelian recombinations, and still others were without doubt only the fluctuating responses of organisms to environment.

After de Vries called attention to mutations, others began to recognize them, and now it is known that in both plants and animals they are frequent, some species producing large numbers. Some are conspicuous, and others not easily recognized; some are structural and others physiologic; some are obviously important to the life of the plant; and others may not affect its success in the struggle for existence. In all true mutations, be they great or small, the new characters result from changes in the genes, and therefore follow Mendelian methods of inheritance. Some of the variations de Vries discovered in *Oenothera* have come to be interpreted by later investigators in ways somewhat at variance with his ideas. Even though they may not all be true mutations, de Vries must be given credit for recognizing them and for stimulating a vast amount of productive research, much of which is still in progress.

Within recent years a degree of success has come in attempts to increase the number of mutations in the laboratory. The most fruitful of these make use of radiations such as exposure to x-rays and radium. The experimenter has no method, as yet, by which to control the type of mutation, but the frequency can be increased many fold. Deeply penetrating radiations change the structure, both chemically and physically, of the chromosomes, and in this way the action of the genes is altered.

Investigators are not in complete agreement as to the part played by mutations in the process of evolution. Many believe with de Vries that these are the variations on which natural selection can act, while others are not fully convinced. Further research will doubtless establish the facts, and bring the disagreement to a close.

Polyploidy. Since the days of Mendel more and more attention has been concentrated on the chromosome with its genes. It is now a familiar fact that any alteration in the chromosome produces variations, and it is believed that these are probably responsible for evolutionary changes. One type of chromosome behavior, known as *polyploidy*, (p. 160), is of special importance in the production of variations, some of which are fully fertile and breed true in succeeding generations. In other words, this is a very important type of mutation. Polyploidy comes about from the fact that at times reduction division fails to occur and consequently gametes form with the unreduced (*diploid*) number of chromosomes. It is customary to indicate the reduced, or haploid number as $1n$, the diploid as $2n$, and the larger numbers as $3n$ (*triploid*), $4n$ (*tetraploid*), etc. Those beyond $2n$ are called *polyploids*. If a diploid gamete enters into fertilization with a haploid one the resulting zygote is triploid ($2n + 1n = 3n$) and the plant that develops from this zygote is called a triploid plant. If two diploid gametes unite, the zygote is tetraploid. By such unusual fertilizations, during a long series of generations it is possible for a haploid number of chromosomes to build up into almost any multiple of itself. As an example, the reduced number in certain cultivated raspberries is 7 and therefore that following fertilization is 14. Other raspberries have, 21, 28, 42, and 49 instead of 14. In like manner 7, 14, and 21 are the haploid numbers of the various types of wheat. All the most important crop wheats belong to the last of these categories. How many haploid sets occur in each of these? The exact time and combination of events which bring about these changes in chromosome numbers in nature are not known, but under laboratory conditions such reduplications are known to occur, and there is no reason to question the assumption that they take place in nature as well. In fact, several of the mutations found by de Vries in the evening primroses have been shown to be of this type.

Within recent years a number of means, especially great changes of temperature, and treatment with certain chemicals, have been devised to increase the frequency of polyploidy. One of these chemicals, called colchicine, is proving to be extremely effective. This substance is applied to various parts of plants in the form of a very dilute solution. When the concentration is great, this solution acts as a distinct poison, but when it is sufficiently dilute, the chemical produces only an anesthetic effect on the protoplasm, making the movements of the chromosomes slow and uncertain during both mitosis and meisosis. In this way the chromosomes frequently fail to separate in a normal manner. The result is that almost every kind of chromosome aberration may arise.

Comparisons of polyploids, however produced, with the diploids from which they arise, show the two always to be more or less distinct. It should be understood that tetraploidy is in itself a most important form of genetic isolation (See p. 170). When once formed, a tetraploid is capable of producing fertile offspring and therefore of perpetuating itself. On the other hand, if it is crossed with the diploid stock from which it was derived, the resulting plants are triploids which are incapable of producing functional gametes. Even though the diploid and its tetraploid form may be growing side by side, they are as completely isolated sexually as if they were far apart. For this reason, any mutation which occurs in either of them makes them correspondingly more distinct. At least theoretically it would be possible for a new species to be initiated in this manner in a single generation.

Some idea of the way in which polyploidy probably acts can be gained by recalling certain facts of Mendelian inheritance. It was said in Chapter 10 that very often dominance is lacking or incomplete. Under these conditions the increase in number of chromosomes carrying an incompletely dominant gene would intensify the resulting characters and produce distinct variations. Likewise, it is becoming evident that a given determiner may affect more than one phenotypic character and that various combinations of genes and the balances between groups of them are important in producing the almost infinite number of modifications observed in nature. Apparently natural selection acts on all variations without regard to their causes.

Other Possible Sources of New Species. A few laboratory experiments may throw light on some of the ways new species may come into existence with or without human interference. One of these studies has been made with the two common garden vegetables, radish and cabbage. These plants belong to the same family but not to the same genus. In other words, they are somewhat closely related but, as would be expected from their appearance, they are very distinct.

Crosses made between these plants by artificial means result in the production of seeds in a considerable number of instances. Many of these seeds are imperfect, but occasional ones give rise to successful plants. These plants have cabbage-like roots and radish-like leaves. They are therefore quite useless as garden crops, but from the standpoint of the biologist they seem to point the way to a possible solution of a part of the species question, for they are fully fertile and capable of perpetuating themselves generation after generation. Here, then, is the origin of a totally new form, entirely distinct from any known species. If such crosses occur among wild plants, when insects or the wind carry pollen from flower to flower, it seems possible that such new, pure-breeding forms may occasionally spring into existence as new species. In fact, there is some evidence that this does sometimes occur.

Another type of mutation that has recently come to be recognized results from displacements and reversals in the positions of chromosomes or their parts. All these positional changes produce mutational variations. Evidence is accumulating that this kind of action may be a fruitful source of the modifications on which natural selection can act, and therefore of evolutionary progress.

The Present-day Status of Evolutionary Thought. Since the beginning of the Renaissance following the Middle Ages, there has been a renewed and growing interest in the question of the origin of species. At the time of Charles Darwin, there was much controversy even among scientists over the relative merits of the theories of direct creation and evolution, but in general the majority held to the direct creation theory. Then came Darwin's remarkable book, remarkable because of the vast amount of material he had assembled during the 20 years he had worked on it and because of the logic he used. The theory of natural selection set the world of biologic research into renewed attack on the problem of the origin of species. The net result has been that biologists as a group have been more and more thoroughly convinced of the validity of evolution as the method by which species have come, and still are coming into existence. That Darwin did not have a complete grasp of the details of the process may be ascribed to the fact that at the time of his death little was known of the cause and method of action of hereditary variation.

This does not mean that evolution is in question, for there is no doubt among the active research biologists that the concept is fundamental. Many attempts are being made to explain the details of the process. These attempts constitute an active field of research at the present time. A very high percentage of modern biologists would probably subscribe to the statement that present evidence points strongly to evolutionary change resulting from mutations which recombine in Mendelian fashion and are acted upon by natural selection. Furthermore, the majority would include polyploidy and other chromosome aberrations as well as isolation as probable additional factors.

Summary. The modern biologist sees continual changes in organisms from generation to generation. "Variation is the most invariable fact in the universe." He sees that child is not exactly like parent, indeed could not be, because the parents are different. He sees in fossils evidence that change has been going on for millions of years. In addition, experimental work shows that divergence takes place as generation succeeds generation, and none of it points to fixity. Thus the entire field of observation and experiment has made it quite impossible for the present-day research biologist to accept direct creation as the explanation of the facts he observes.

It is true that the underlying laws of variation are far from being completely understood, but the fact of variation itself can not be overlooked. Explanations of phenomena may be correct only in part, or they may be quite mistaken, but the facts of nature are still in operation, only waiting more complete

understanding on the part of investigators. The discarding or revising of a mistaken explanation in no wise discredits the facts one is trying to explain, and if present theories regarding the active forces bringing about evolutionary changes should prove, in part, untenable, this situation could not in the least prevent the continuation of evolution itself.

SUPPLEMENTARY READINGS

Andrews, "Ancient Plants and the World They Lived In."
Arnold, "An Introduction to Paleontology."
Darwin, "The Origin of Species."
Osborn, "From the Greeks to Darwin."
Seward, "Plant Life Through the Ages."
Ward, "Charles Darwin."

Chapter 12

KINSHIP AND CLASSIFICATION

Modern biologists are striving to develop a scheme of classification of plants and animals that is based on the actual genetic and evolutionary relationships among living things. This short chapter is devoted to the task of elucidating a few of the fundamentals that must be depended upon in such an undertaking and to an outline of the plant kingdom built on this foundation. Succeeding chapters will erect the superstructure.

The following four heads of sections constitute a summary of the most important points that are treated here:

Natural and Artificial Classifications
Early Attempts to Classify Plants
Technical and Common Names
An Outline of the Plant Kingdom

Any group of objects can be classified. In fact, we continually, though often unconsciously, organize in our minds the multitude of details of our surroundings. We think of objects as being living and nonliving; as minerals, plants, and animals; as solids, liquids, and gases; and as members of multitudes of other categories. Whether we make our groupings thoughtlessly and inaccurately, or purposely and with precision, all of us continually apply some criteria by which we classify our surroundings.

Classifications of all kinds are based on comparisons and contrasts, and the most useful and most lasting ones depend on a sound knowledge of the true relationships between the objects that are being classified. Application of this principle to plants and other living things shows that the most reliable form of classification that has been devised in the field of biology is based on genetic kinship. Genetic kinship means that those organisms whose gene complexes are the most nearly alike are the most closely related to each other; and, on the contrary, those that have received very different sets of genes from their ancestors are correspondingly more remotely related to one another. In previous chapters it has been said repeatedly that differences in the genes result in differences in form and physiologic activity. Applying this principle, it is obvious that beans and peas are much more closely related to each other genetically than either of them is related to asparagus, and that muskmelons bear a much closer kinship to pumpkins than to palm trees.

Natural and Artificial Classifications. Natural classification is a means of expressing actual relationships while artificial ones are merely convenient ways of distinguishing objects without showing their true similarities.

Examples of artificial classifications of plants are those that divide them into trees, shrubs, and herbs; into those that grow in wet, moist and dry locations; and those with various colors of flowers, without regard to genetic kinship.

The unit of natural classification is the *species*. A species is a group of individuals that are similar to each other and are capable of producing offspring

essentially like themselves, but are sufficiently distinct from other groups to make the production of fertile crosses unlikely under natural conditions.

The number of species of plants is unknown but more than a third of a million have been named and about 5,000 new ones are discovered and added to the list every year. Some plants are so very small that high magnification with a microscope is required even to see them, while others, such as the largest trees, weigh several tons. Some fully mature plants are only single cells so poorly organized that it is impossible even to distinguish between nucleus and cytoplasm, while at the opposite extreme are the most complicated of flowering plants.

No one person has seen examples of all the known species of plants and such an undertaking would be both useless and impossible of accomplishment. Yet every student of botany needs to be acquainted with a few members of a wide variety of types. Such acquaintance can be acquired by grouping together those kinds that are most nearly alike and becoming familiar with at least one representative of each important group.

Species which closely resemble one another are placed in the same *genus* (plural, *genera*). As examples, all the species of willows are placed in the one genus, *Salix;* those of onions in *Allium;* the various roses in *Rosa;* and the pine trees in *Pinus*. In like manner, all the hundreds of thousands of species are grouped into thousands of genera.

Early Attempts to Classify Plants. Apparently man was first interested in plants as sources of food. Each kind, therefore, was classified as edible or inedible. Then some came to be used as remedies for disease, and the added lists of those to be used as cures for fever, for pains in various parts of the body, and for other ailments gained some currency. As civilization advanced certain of the ancient Greeks began to group plants, not by their more or less temporary uses, but by their actual characteristics. These classifications were mostly very simple, and included such groupings as those with leaves or without them; woody or herbaceous plants, etc., but they were the forerunners of the more accurate ones to be developed as knowledge increased.

As time went on mankind gradually built up a number of categories in which various kinds of plants were placed. These pioneer attempts at classification had their temporary value but were all at fault because they dealt with superficial matters rather than with fundamental relationships and for that reason they were artificial classifications.

Though their shortcomings are recognized, some of these are still in use because they are sometimes very convenient and simple. As examples, there are excellent reference books on useful and medicinal plants; on trees and shrubs; on poisonous plants; on fruits; on ornamentals; on range plants; and a long list of others.

As the science of botany developed, more systematic effort was put forth to formulate accurate and well-founded means of classifying plants and animals. At first, these attempts were very simple, and according to modern standards were far from successful. Nevertheless, gradual progress has been made in approaching a satisfactory basis of classification. At the present time botanists are trying with some success to produce an outline of the plant kingdom that will be in full agreement with genetic and evolutionary relationships. The remainder of this, as well as the next eight chapters, are devoted to a somewhat detailed account of such an outline.

Technical and Common Names. During the time when systematic classification was beginning to develop there was on foot a movement to give precise names to plants. For long periods of time the earliest botanists had no method of designating any species they wished to discuss except by writing descriptions, for there were no universally accepted names. Each scientist therefore found it necessary to describe in Latin—the language of the scholar of the day—those characteristics of the plant in hand that seemed to him to be most important. As might be expected, it was only seldom that two persons used the same description. Besides, these descriptions were often cumbersome and difficult to interpret.

From time to time some botanist used two names to represent a given species. This device helped to simplify the situation, but lacked system. Then in 1753 the great Swedish botanist, Linnaeus, published his "Species Plantarum." In this book he

introduced some of the needed order into the prevalent chaos by the simple expedient of giving every species a name made up of two parts. At present, as a result of the general adoption of this principle, instead of a lengthy description it is necessary only to write *Quercus rubra* for red oak or *Acer saccharum* for sugar maple to be fully understood by botanists everywhere.

By this device Linnaeus placed in the hands of the botanist a simple tool that has proved especially useful as a method of indicating modern ideas of relationships among plants. It is recognized now, in a way that it was not earlier understood, that all oaks are truly related to each other because they have in common very large numbers of gene complexes. This relationship is indicated by placing all of them in the genus *Quercus*. In like manner, the maples are *Acer*, and the willows, *Salix;* and so throughout all groups of plants, the most closely related species are placed in the same genus.

Modern practice follows the lead of Linnaeus and gives every organism a technical name composed of two parts: the genus to which it belongs, and a descriptive or limiting term, sometimes called the specific name. This kind of designation is known as *binomial nomenclature.*

As examples, the complete technical name of the sugar maple is *Acer saccharum* and of red maple is *Acer rubrum*. The name of a genus always begins with a capital letter and is usually a Latin noun. The specific name modifies the noun and, with few exceptions, begins with a small letter. Continuing the illustration, *Acer* is the Latin word for maple, *saccharum* refers to the sugar which is obtained from the sap of this species of tree, and *rubrum* means red.

To the person who is first meeting technical names they seem strange and difficult. For this reason students frequently suggest that such common English words as maple, willow, and rose are more satisfactory than the equivalent *Acer*, *Salix*, and *Rosa*. In reality both types are useful, each for its own purpose.

Common names are convenient in general discussions because they are much used and are, therefore, familiar to most people. In addition, they are frequently sufficiently descriptive to make them easy to remember. Their disadvantages come from the fact that a given one often applies to a considerable number of different species. Sometimes these species are not at all closely related to each other. As an example, sycamore refers to three very diverse kinds of trees in three different geographical localities. In the eastern Mediterranean region it applies to a fig tree, in England to a maple, and in the United States to the familiar white-barked trees that grow along stream courses across the southern half of the country.

Other disadvantages of common names are that they are seldom used in more than one language and tend to be rather local within a language, therefore having little meaning beyond a limited community. Thus, *Asclepias tuberosa*, a milkweed with attractive orange colored flowers, is known by at least a dozen English names, a few of which are butterfly weed, pleurisy root, orange root, yellow milkweed, orange swallow root and Indian posy.

Finally, it is only those plants that attract general attention that usually acquire common names. For this reason crop plants, ornamentals, those that are used for medicinal purposes, those that are known to be poisonous, and weeds, all have recognized names wherever they grow. In contrast, many others, especially those that are not commonly noticed, have no such names.

Obviously, then, while common names are convenient, there are several reasons why the botanist is forced to make considerable use of technical terms in the interests of accuracy.

In order to overcome the deficiencies and uncertainties arising from the use of local expressions, scientists gradually developed technical designations for all known species of plants and animals. Latin is probably better adapted to this use than any other language because it is now seldom used as a medium of conversation and is, therefore, not growing and changing. Plant names need to have the same meaning at various times and places, and the use of an unchanging language is almost obligatory.

An Outline of the Plant Kingdom. Just as closely related *species* are grouped into a single *genus*, in like manner closely related genera are placed together to form a *family*. Likewise, groups

of increasingly greater size are, step by step, *orders, classes* and, finally, *divisions.*

The plant kingdom as a whole can be broken up in a number of ways into a few large sections. These are the *divisions.* Numerous attempts have been made to recognize and name such categories, basing the classification on natural relationships. One of the earlier of these schemes of classification is given on p. 4 and again in the left hand column of the following outline. This classification was first proposed by Eichler in 1886, about seventy years ago. It so well summarized the ideas of plant classification of the time that it came quickly into use with only minor deviations from his original outline. Generation after generation of botanists became accustomed to it and thus what had been a new classification developed into a firmly grounded tradition. The weakest point in this classification lies in the fact that it took no account of paleobotany. Already there had been reports on plant fossils which were to play important parts in future considerations, but their significance seems to have been missed. Later, increasingly numerous discoveries were to make untenable some parts of the Eichlerian classification. When these, including more accurate interpretations of plant anatomy, the life cycle, genetics, and biochemistry are all brought to bear on the problem, the column at the right ensues. It begins with the simplest, most primitive divisions and indicates relationships, in

Classification of the Plant Kingdom

Traditional Classification	*Newer Classification*	
Divisions Classes Subclasses	Divisions Classes Subclasses	
1. Thallophyta		
a. Algae		
(a) Schizophyceae	1. Schizophyta	Fission plants
(i) Cyanophyceae	a. Cyanophyceae	Blue-green algae
(ii) Schizomycetes	b. Schizomycetae	Bacteria
(b) Chlorophyceae	2. Rhodophyta	Red algae
(c) Rhodophyceae	3. Phaeophyta	Brown algae
(d) Phaeophyceae	4. Chrysophyta	Golden algae
	5. Protochlorophyta	Green algae
b. Fungi	6. Mycophyta	Fungi
(a) Phycomycetes	a. Phycomycetae	Alga-like fungi
(b) Ascomycetes	b. Ascomycetae	Sac fungi
(c) Basidiomycetes	c. Basidiomycetae	Club fungi
(d) Fungi imperfecti	d. Fungi imperfecti	Fungi with unknown or incomplete life histories
c. Lichens	e. Lichens	Lichens
2. Bryophyta	7. Bryophyta	Bryophytes
a. Hepaticae	a. Hepaticae	Liverworts
b. Musci	b. Musci	Mosses
3. Pteridophyta		
a. Psilophytineae	8. Psilopsida	Psilopsida
b. Equisetineae	9. Sphenopsida	Horsetails and scouring rushes
c. Lycopodineae	10. Lycopsida	Clubmosses
d. Filicineae	11. Pteropsida	Pteropsida
4. Spermatophyta	a. Filicineae	Ferns
a. Gymnospermae	b. Gymnospermae	Gymnosperms
b. Angiospermae	c. Angiospermae	Angiosperms
(a) Dicotyledonae	(a) Dicotyledonae	Dicotyledons
(b) Monocotyledonae	(b) Monocotyledonae	Monocotyledons

so far as it is possible to interpret them, step by step up to the most complex plants. The reasons for these interpretations of kinship will gradually appear with detailed study of individual forms in succeeding chapters.

These are the important groups of plants; a few others that are rare or seldom studied in elementary courses are omitted.

In order to grasp the significance of the newer scheme of classification it is necessary to clarify some of the underlying concepts on which it is built. First of all, the basic differences between natural groups of plants are, strictly speaking, hereditary. If these differences were only the variations brought about by fluctuations of the environment, they would be so changeable that they could be of no value in determining relationships. Stated in another way, the natural groupings of plants result from important differences in gene combinations.

One illustration will indicate the meaning of this statement. It is well known that monocotyledons develop one cotyledon in each seed, and have scattered steles in the stem and parallel veins in the leaves. These characteristics are clearly the results of certain gene combinations which control the peculiarities of growth, for there is no known change of environment which will influence the number of cotyledons in a seed, or change the type of stele, or alter the venation in the leaves.

What is the nature of these gene combinations which act so continuously to maintain the unvarying sets of characteristics which distinguish one division, or class, or order of plants from all others? The only present explanation is that all members of these groups are homozygous for the genes necessary to produce these fundamental peculiarities. In other words, the gene combinations which produce the set of characteristics of any established group are handed down through the generations to every normal member of that group. Other genes may be heterozygous, bringing about the minor variations such as those dealt with in the chapter on plant genetics.

Because some of the relationships among plants are unknown, or known only in part, several schemes of classification are in use that are not in full agreement with each other. Nothing but more knowledge can solve some of the problems involved.

Whatever the number or character of the divisions used and whatever criteria are employed in separating them, the series of steps in the classification of any organism remains the same. In other words, beginning with the largest group, there are in descending order, divisions, classes, orders, families, genera, and species.

To illustrate the relationships of the large and smaller categories within the plant kingdom, two examples will be included here:

Plant Kingdom		
Division	Pteropsida	Pteropsida
Subdivision	Angiospermae	Angiospermae
Class	Dicotyledonae	Monocotyledonae
Order	Rosales	Liliales
Family	Leguminosae	Liliaceae
Genus	*Trifolium*	*Allium*
Species	*repens*	*cepa*
Common name	White clover	Onion

Every individual plant falls naturally into a similar set of groupings. That is to day, it belongs to a species, and every species is included in a genus, every genus in a family, every family in an order, every order in a class and every class in a division. In the succeeding chapter the most primitive division of the plant kingdom is treated in such a way as to follow relationships in classification.

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Eames, "Morphology of Vascular Plants."
Gortner, "Outlines of Biochemistry."
Smith, "Cryptogamic Botany."
Swingle, "A Textbook of Systematic Botany."

Chapter 13

SCHIZOPHYTA: FISSION PLANTS

This chapter deals exclusively with one division made up of two classes, as follows:

Schizophyta
  Schizomycetae, bacteria
  Cyanophyceae, blue-green algae

The earliest fossil records of both bacteria and blue-green algae date back to Proterozoic times. It is not known how long these primitive forms had been on earth before the earliest fossils were formed, but there is ample evidence that in the world of life members of the schizophytes have been playing important parts without cessation over a span of about a billion years.

Paleozoic Age	
Proterozoic Age About 1 billion years ago See p. 169	The most ancient records seem to be bacteria and blue-green algae

Blue-green algae of the present-day are distinct in several ways from all other plants that can carry on photosynthesis. The following chart will summarize these peculiarities.

Cellular Structure	*Pigments*	*Food Reserves*
No organized nucleus Pigments not in plastids	Chlorophyll Carotinoids Phycocyanin (and sometimes phycoerythrin)	Glycogen or "animal starch"

Blue-green algae have the following similarities to bacteria:

Neither has organized nucleus
Neither has sexual reproduction
Both multiply by fission

The following are the main topics discussed in this chapter:

Blue-green Algae
  Gloeocapsa
  Merismopedia
  Oscillatoria
  Nostoc and *Anabaena*
  Gloeotrichia
  Importance of Blue-green Algae

The blue-green algae and their near relatives, the bacteria, together constituting the Schizophyta, are probably the most primitive plants, if not, indeed, the most primitive organisms of any kind on earth today. Both the name, *fission plants*, and the technical equivalent, Schizophyta (*schizein*, to split; *phyton*, plant) come from the fact that the cells divide, not by mitotic divisions which are characteristic in higher plants, but by simply splitting in two. The history of this division of the plant kingdom extends back through the ages of time to periods almost unbelievably remote, for there are no known fossil records more ancient than those of blue-green algae. Some of these records are somewhat less than one billion years old (see p. 169). The kinds of living things that antedated these earliest fossil forms are unknown but the records of blue-green algae extend from those ancient times to the present moment with relatively little variation. No other plant group, unless, perhaps it is the bacteria, has left a series of fossils showing so little change down through the ages.

There are those who believe that some of the schizophytes of ancient times varied to such an extent that they became the originators of other plant groups. If such changes did occur, the new forms ceased to belong to this division and took on the more specialized characteristics of higher groups.

Regardless of these theories, the organisms that belong to the division, Schizophyta, represent a type which appeared early in the history of life on earth and which today are the simplest known forms of living things.

At this point it should be understood that the name *algae* refers to any of the most primitive plants that have chlorophyll, but does not imply either kinship or a lack of it between the various ones. That is to say, the word algae as used in this classification is little more than a common name. Among the most conspicuous forms are the pond scums and sea weeds. Many others are microscopic and are not often noticed except by those studying them.

BLUE-GREEN ALGAE

Occurrence. The blue-green algae or Cyanophyceae (*kyanos*, dark blue; *phykos*, alga) are to be found in almost any place where there is continuous moisture, and occur even in arid regions where they may remain dry for long periods of time between the occasional rains.

The bluish-green growth that sometimes forms on flower pots and wet floors in greenhouses; the tenuous layer of various colors, often called "water bloom," that floats on ponds and small lakes in summer; the yellowish slime attached to stones in the rapids of streams; the unattractive greenish or brownish floating masses on rivers and lakes; and the dark coating inside watering troughs, are usually made up largely of blue-green algae. Wet

Mamouth Hot Springs, Yellowstone National Park. Large quantities of blue green algae are growing in this steaming hot water.

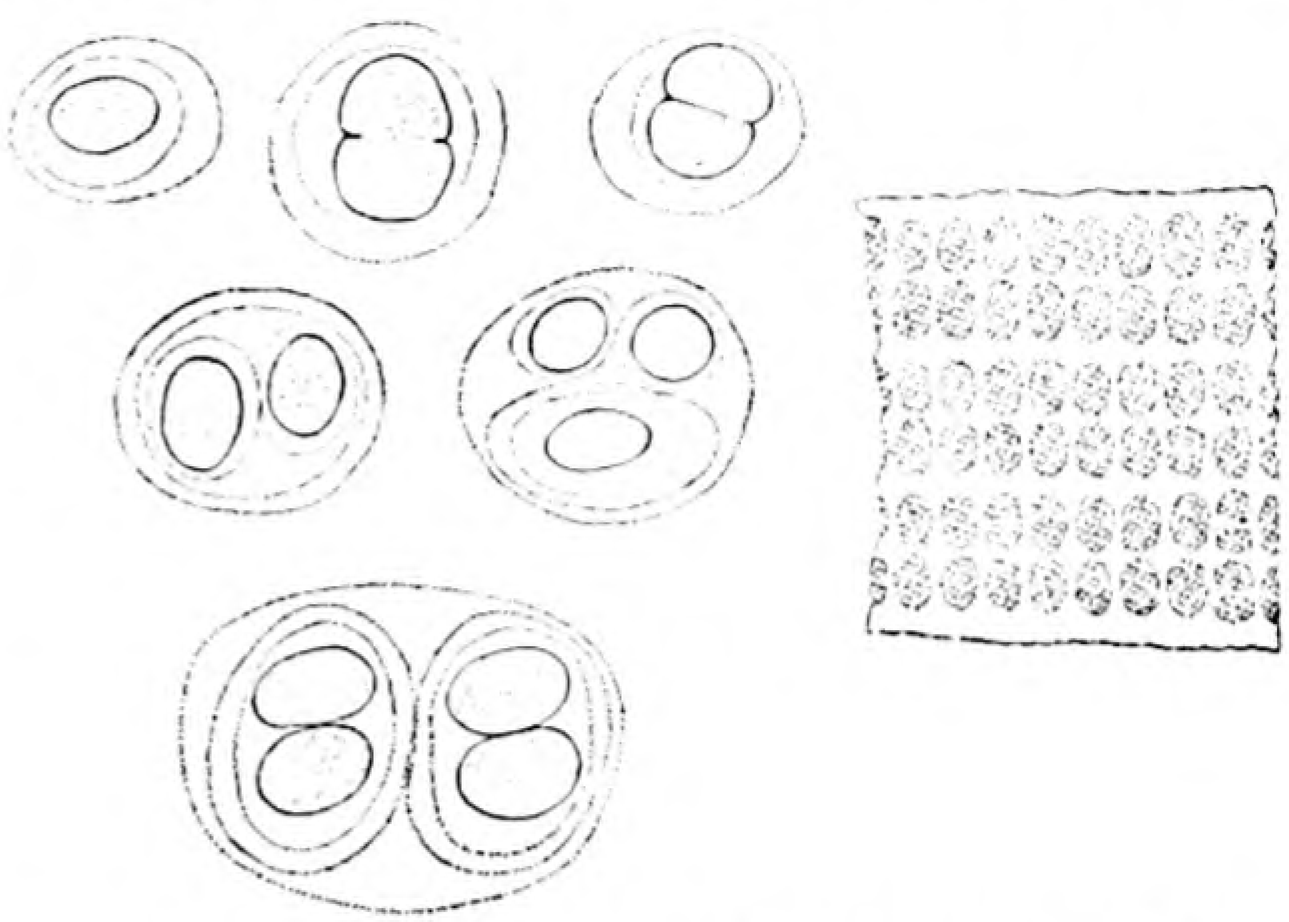
soil near streams and ponds is a favorable place for many of them and numerous species inhabit the surface layers of soil, although they are seldom seen without special search. Some grow freely in hot springs and geyser pools where the temperature is far too high to be comfortable to the hand. A large amount of decaying organic material in the water seems to be favorable to most of them, and a few species thrive in water which has a mineral content too high for most other plants.

Organization. The peculiar dull color usually shown by these algae ranges from almost black to a pale green and is due to a combination of varying amounts of chlorophyll and carotinoid pigments together with a bluish coloring substance known as *phycocyanin;* sometimes there is, in addition, a reddish pigment called *phycoerythrin.* The color resulting from this mixture of green, yellow, blue, and red is made even less attractive by the deposits of mud, decayed organic material, and mineral substances which may partly surround the plants. Sometimes, as in hot springs, these algae display cleaner and more brilliant hues, but practically never the clear, bright, grass-green of many of the other algae.

When rubbed between thumb and fingers most species of blue-green algae give the sensation of a heavy machine oil or of a thin jelly. The reason is that the cell walls are commonly made of a thick layer of colloidal material that is closely related, chemically, to pectin.

These plants are considered to be very primitive because of their simple organization and mode of reproduction. While the cells appear to contain nuclear materials (perhaps chromatin) scattered about through the cytoplasm, they do not have organized nuclei. Members of the two classes of the Schizophyta are the only plants, indeed the only known organisms, in which well-developed nuclei do not occur. Again, all of the more specialized chlorophyll-bearing plants have definite chloroplasts, but the Cyanophyceae have chlorophyll and other pigments in solution in the outer layers of the cells but do not have definite plastids. The products of photosynthesis never take the form of ordinary starch. Instead, glycogen or "animal starch," similar to that commonly found in the tissues of animals, is the usual form of reserve carbohydrates in all the Cyanophyceae.

Reproduction within the group is also extremely primitive. In no case is even the simplest type of sexual reproduction known. Instead, in the multi-



(*Left*) *Gloeocapsa*, showing various stages in cell division and the layers in the very thick gelatinous walls. (*Right*) *Merismopedia*, with cells arranged in a "checker board" pattern and held together by their gelatinous walls.

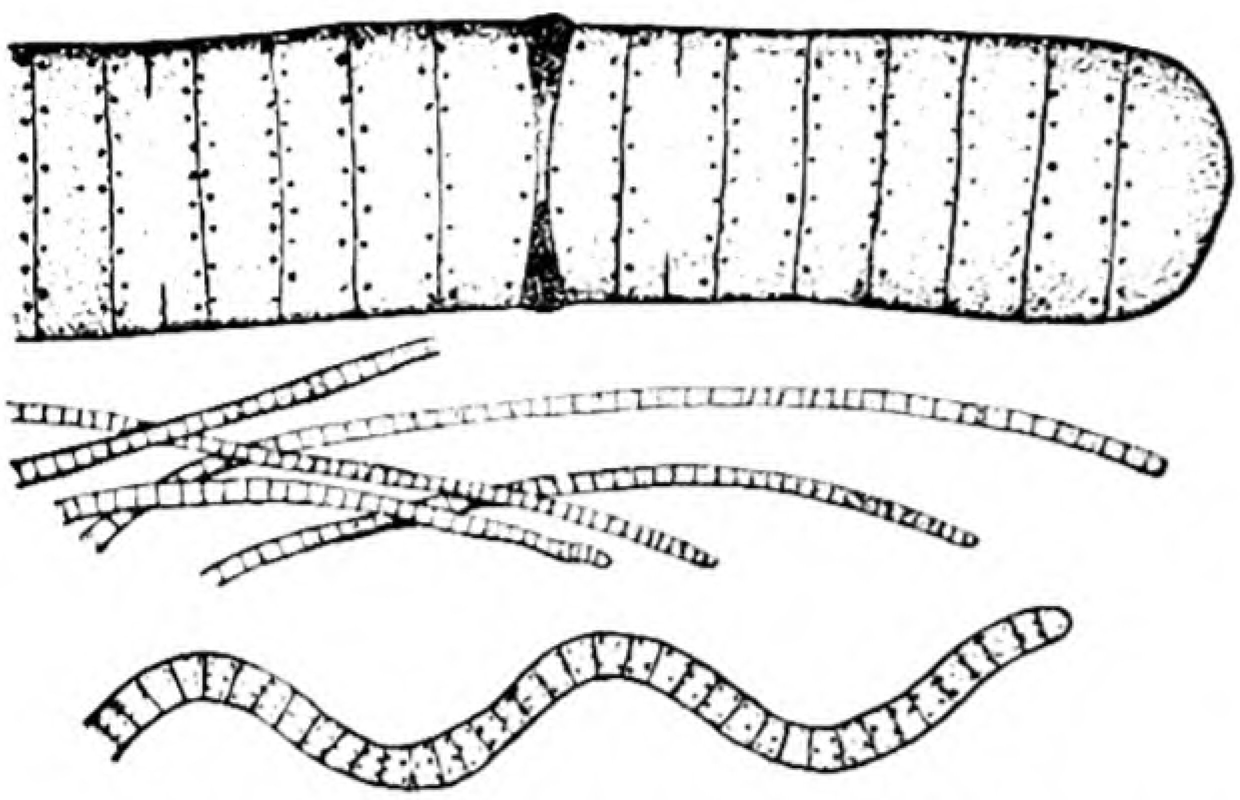
cellular forms, groups of cells may break off from their neighbors and start new plants, or in the one-celled species, the single cell divides, making two new individuals from one.

Even cell division is extremely primitive. The protoplast appears only to constrict, organizing a new wall and separating itself into two parts. This type of division is called *fission*.

Examples of Blue-green Algae. GLOEOCAPSA. One of the simplest genera of blue-green algae is *Gloeocapsa* (*gloia*, glue; *capsa*, case). The individual is a single cell surrounded by a thick mass of jelly-like, pectic material which shows evidence of having been secreted in layers. As fission occurs, the new cells are often held together for a time by this gelantinous substance, making irregular colonies, but the cells are apparently entirely independent of one another. *Gloeocapsa* grows most frequently in the form of yellow-green gelatinous layers on wet rocks, on flower pots in green houses, or sometimes as irregular floating flakes in water.

MERISMOPEDIA. The individual cells of this genus are similar to those of *Gloeocapsa*. Its most

obvious difference from that form lies in the fact that the cells of *Merismopedia* are arranged in a single layer, and are so placed as to appear somewhat like the squares on a checker board. This peculiar arrangement results from the fact that all



(*Top*) Large species of *Oscillatoria* showing cellular structure of the filament. Two of the cells are dividing, the walls constricting from the outside. The larger, dark spots are granules of phycocyanin. The lens-shaped object near the center is a gelatinous separation disc. The filament would break especially readily at this point. (*Center*) A species of *Oscillatoria* with long cells, as seen with low magnification. (*Bottom*) A filament of *Arthrospira*, showing the characteristic spiral form.

the cells of a given colony commonly divide at about the same time and in the same direction. Each succeeding division is at right angles to the one just before, and the gelatinous walls hold large numbers together in the form of a thin sheet. *Merismopedia* grows, mixed with other microscopic floating algae, collectively called plankton, in ponds, lakes, and ditches.

Oscillatoria. This is one of the most widespread and best known genera of the Cyanophyceae. It is found in polluted water and on wet ground the world over. When layers of it coat the soil or rocks in shallow water, bubbles of gas, largely of oxygen from photosynthesis, frequently accumulate, tearing fragments loose and carrying them to the surface where they remain in dark, floating masses. One species has, in addition to chlorophyll and carotinoid pigments, such large amounts of the red pigment, phycoerythrin, that the alga gives a reddish color to the water in which it grows. The Red Sea takes its name from this species of *Oscillatoria* which at times is very abundant in its waters.

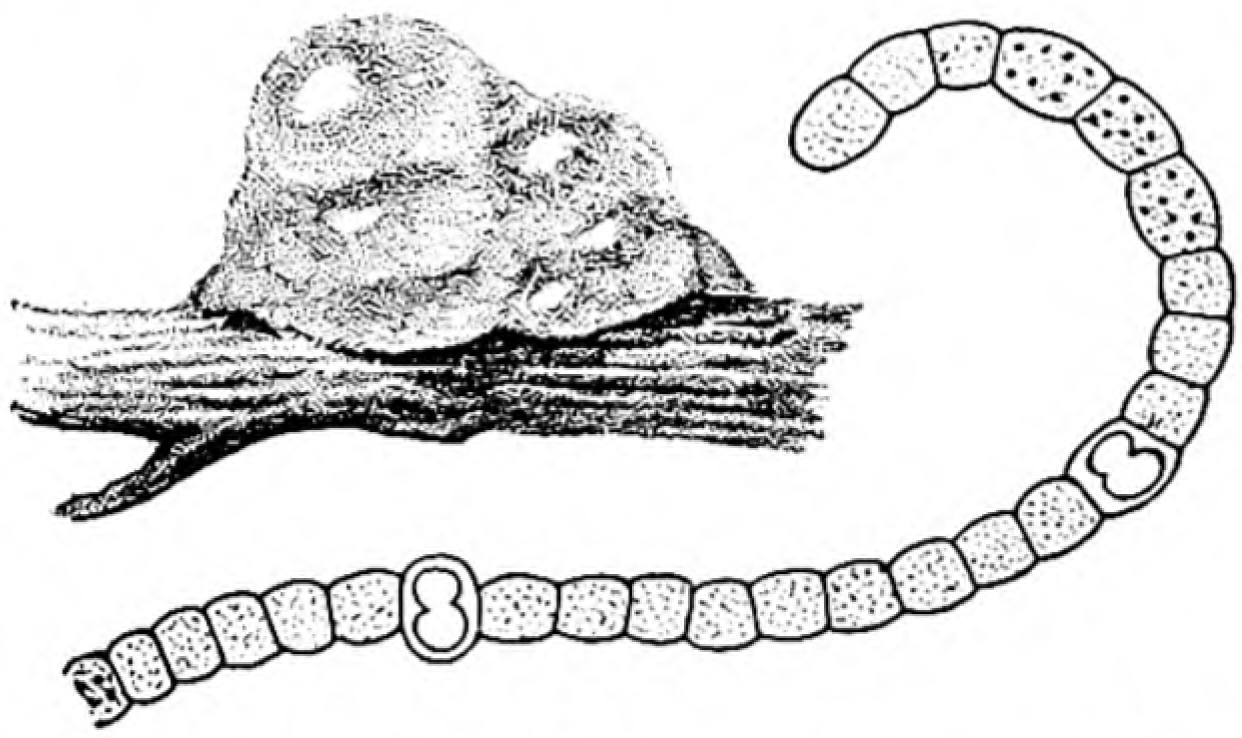
The individual plants are simple filaments or threads made up of disk-like cells or sometimes longer ones, placed together like a pile of coins, with the whole surrounded by a thin, tough gelatinous sheath. The end cells are more or less rounded, and when a filament is broken or when a protoplast dies the adjacent ones become rounded on the free side, indicating that all would tend to be spherical if they were not compressed by contact with others as they are held in the sheath.

As in all genera of the Cyanophyceae, the cells of *Oscillatoria* divide by fission. A thin, ringlike extension grows inward from the peripheral wall, gradually separating the protoplast into two parts. Division always occurs at right angles to the length of the filament, which consequently remains only one cell wide. When a cell dies or, as sometimes occurs, a gelatinous "separation disk" forms, the filament is weakened, causing it to break in two, thus making two individuals. No other method of reproduction is known in this genus.

Since there is practically no differentiation in the cells and they are so little dependent upon one another, each of them, instead of the whole thread, might be regarded as the individual were it not for a peculiar motion of the filament which acts as a unit. If a small mass of the plant is placed in a few drops of water and left undisturbed for a short time, the filaments slowly adjust themselves so that they radiate out in various directions. The method by which they move is not well known, but with the microscope they can be seen to creep endwise, to roll over slowly, and to wave jerkily to and fro like an unsteady pendulum. It is from this oscillating movement that the genus takes its name. A considerable number but not all the Cyanophyceae, have some powers of motion. *Arthrospira* is a genus closely related to *Oscillatoria*, but is different from it in that *Arthrospira* plants are bent into the form of a regular spiral. Members of this genus may be found occasionally in stagnant or brackish water.

Nostoc and Anabaena. These genera which often occur together, are so much alike that they are frequently difficult to distinguish from each

other. The filaments of the former, however, are covered with a firm gelatinous sheath that causes them to cling together in tough rubbery masses which may take almost any shape, frequently forming balls as large as an inch in diameter. One



Nostac. (*Left*) Gelatinous mass as seen without magnification. (*Right*) Filament as seen with high magnification showing resting cells and two heterocysts. The chains of beadlike cells between heterocysts are hormogonia.

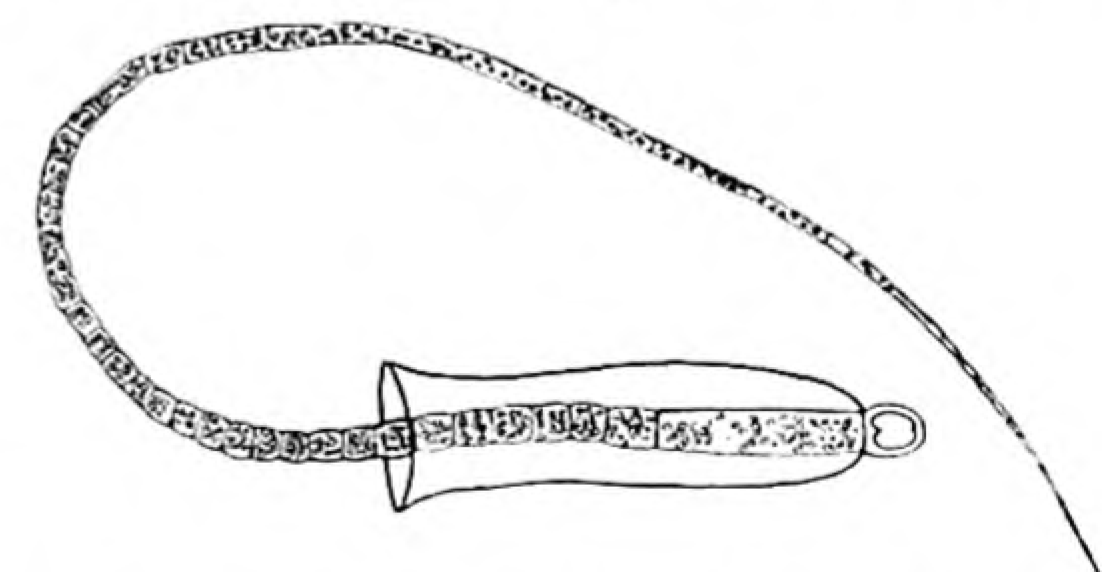
species, *Nostoc commune*, makes a rubbery layer on moist ground and occurs in various parts of the world. In arid regions it imbibes water and grows after rains but soon dries and takes on the characteristics of dark brittle fragments of dried glue. The majority of species live in ponds, lakes or streams. The filaments of *Anabaena* have a thin sheath, or almost none at all and do not remain attached to each other, but float in shapeless layers on pools, ditches and lakes.

When examined with the microscope the filaments of both these genera resemble strings of bluish-green beads, with here and there large, yellowish, thick-walled cells known as *heterocysts* (*heteros*, different; *cystis*, cell). Very little is known about the function or significance of the heterocysts, but in some species they cause weak places in the filament. Short chains which are left when a filament breaks up at its heterocysts sometimes wriggle out of the mass and travel for a short distance and start new colonies. These simple reproductive vegetative fragments are known as *hormogonia*. An occasional cell, after enlarging slightly and becoming gorged with food, forms a thick wall and changes into a *resting cell* which may remain viable for many years. It may be carried long distances in water or on the feet of aquatic birds and other animals or may be blown by the wind when dry, only to begin growth and in this way to reproduce the plant when suitable conditions are encountered.

GLOEOTRICHIA. This genus represents the highest specialization found in the blue-green algae. The individual is a long, tapering, whip-like filament with the last cell on the larger end differentiated into a heterocyst, and the next one sometimes forming a resting cell which is commonly surrounded by a gelatinous sheath. At the smaller end of the filament the last cell narrows into a thin, microscopic bristle. The sheaths tend to merge, forming small spherical colonies with the heterocysts at the center and the tapering filaments pointing outward in all directions. The colonies cling to plants or float freely in the water.

Importance of Blue-green Algae. Apparently the members of the Cyanophyceae furnish relatively little food for animals. It is true that fish occasionally eat them when they are growing with other water plants, but even then they appear not to constitute a large percentage of the food of these animals.

When, as sometimes occurs, blue-green algae become numerous in the reservoirs containing city water supplies, they produce flavors and odors that are distasteful. While they are not definitely known to be a hazard to health they must be held in check



Gloeotrichia, showing heterocyst at larger end; dark resting cell surrounded by gelatinous sheath; and whip-like form of filament.

by various means in order to keep such water supplies acceptable to the users. It is even possible that some species may be poisonous to human beings, because farm animals have been killed by drinking water badly contaminated with certain

forms of these algae. Such reports have been recorded from time to time during the past century and from many parts of the world, including Australia, Canada, South Africa, Colorado, Minnesota, and North Dakota. Thus far the toxin has not been identified.

Nutrition. Blue-green algae carry on photosynthesis because they have chlorophyll and live in places where carbon dioxide, water, and light reach them readily. Instead of forming food reserves of starch, as most plants do, they organize glycogen or "animal starch," and small amounts of oils. With respect to reserve foods, therefore, these plants show a physiologic similarity to animals. *Nostoc* is known to fix nitrogen, a capacity well known in certain of the soil bacteria.

The primary interest in the Cyanophyceae, so far as a study of the elements of botany is concerned, lies chiefly in their probable genetic relations to other groups. Therefore, keeping their extremely primitive characteristics well in mind, a study may next be made of their nearest relatives, the bacteria.

BACTERIA

Organization. The division, Schizophyta, includes the two classes, Cyanophyceae already discussed, and Schizomycetae, the bacteria.

Like the word "algae," the name "bacteria" is a semipopular one that refers to a vast assemblage of organisms somewhat similar to one another but which seem to have evolved from several sources. In other words, biochemical studies indicate that the organisms commonly called bacteria are not all closely related to each other. These discussions, therefore will be limited chiefly to the "true bacteria" whose relationships seem to be definitely with the blue-green algae.

While the bacteria average very much smaller than the members of the Cyanophyceae, they assume the same general shapes and types of groupings as do the blue-green algae. Some of them are spheres, others are straight rods, and still others are spirals. Additional evidences of relationship of the true bacteria to blue-green algae come from the facts that in neither group has an organized nucleus been demonstrated; the common method of reproduction in both is by simple fission; and certain members of both are capable of organizing thick-walled resting cells that remain alive for relatively long periods of time even under the extremely hard conditions of drying and high temperatures. In size bacterial cells range from some very large ones which compare favorably with some of the smallest of the blue-green algae, to certain of the cocci (spheres) not more than 0.15 μ in diameter. Because of the limitations of even the best of the light microscopes it has been impossible to answer many of the most important questions about the bacterial cell. Now, with the advent of the electron microscope and the large number of new techniques that are being introduced in preparing objects for study, it is possible to speak with more assurance than ever before. The following outline will summarize the present state of such knowledge:

1. The cytoplasm is enclosed by a plasma membrane which pulls away from the wall when the cell is plasmolyzed. In these respects the bacterial cell is similar to the cell of higher plants.
2. At least one nucleus containing chromatin is present; sometimes there are several, but there is no nuclear membrane.
3. Enclosing the cell is a wall of cellulose or some related polysaccharide, sometimes with the addition of nitrogenous and fatty radicals.
4. A slime layer in the form of a gelatinous coat of various thicknesses surrounds the wall. When firm and thick it is called a *capsule.* This is constructed largely of polysaccharides but varies greatly.
5. Cell division: The first indication that a cell is about to divide is an inward growth of the plasma membrane forming a plate across the middle, followed by a cross wall which splits this plate. When the cross wall splits apart, two new, completely organized bacterial cells exist. The question still remains as to the action of the nuclei during these changes. A few investigators have reported chromosomes, but others have questioned this interpretation. Complete agreement will be

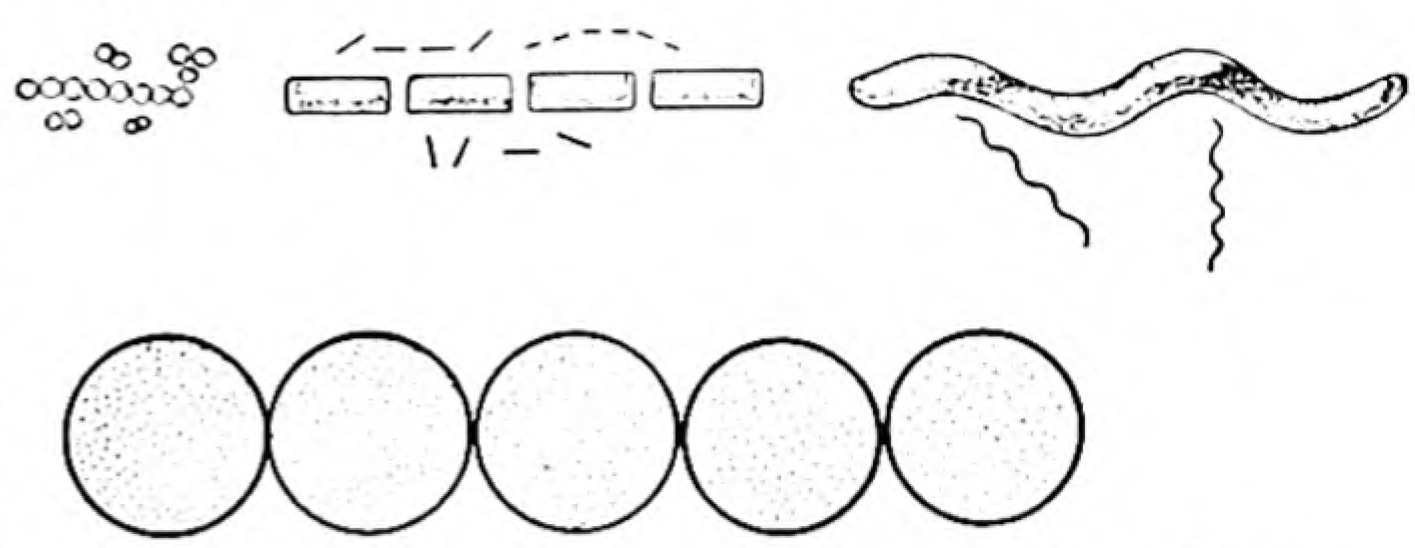
reached when consistent results in the hands of many critical investigators have been achieved.

The greatest differences between blue-green algae and bacteria appear to be that the bacteria have no chlorophyll, are much smaller and, in some species, have flagella by which they can swim. The similarities are so great that it would seem probable that a few changes in the genes in either or both of these groups, occurring down through the ages could account for all the differences. Variations that breed true in these plants are not purely hypothetical, for mutationlike changes are occasionally met by investigators in the field of bacteriology. Such gene changes may, presumably, also occur in the Cyanophyceae, but because of their slight economic importance they have not been studied over long periods of time in great detail in the living condition. For this reason it would be easy to overlook such mutations as might occur.

Nutrition. Since bacteria do not have chlorophyll, their food supply must come from sources different from those of the blue-green algae. With the exception of a few rare forms described at the end of this chapter, all bacteria depend for food on organic materials from sources outside themselves. The great majority secrete enzymes that digest nonliving plant and animal bodies. These are called *saprophytic bacteria* (*sapros*, rotten; *phyton*, plant) and their digestive activities bring about the decay of the materials in which they grow. The products of digestion are absorbed and used in their metabolism.

It should be understood that very many kinds of bacteria take part in the decay of any plant or animal body. Certain ones produce secretions that digest cellulose; others bring about the partial breakdown of lignin, or of fats, or of certain proteins; and still others produce enzymes that act on some one of the end products of a previous step in the process. Decay, then, is in reality a chain of reactions brought about by a complex series of microorganisms, each contributing its bit to the total process.

Other bacteria take food at the expense of the living cells of plants or animals. These are called parasites (*parasitos*, eating at the table of another). Many diseases result from the activities of parasitic bacteria. A few bacterial diseases of human beings might be mentioned, as for instance, typhoid fever,



Bacteria of various types. (*Left*) Cocci. (*Center*) Bacilli. (*Right*) Spirilli. (*Bottom*) Cells of *Nostoc* drawn to same scale.

cholera, tuberculosis, pneumonia, tetanus, boils, and scarlet fever.

In contrast with animals, in which bacteria cause the majority of diseases, plants are subject to relatively few bacterial infections. Some of these, however, are very important to gardeners and horticulturists.

One of these diseases is called *fire blight*. It attacks apples and pears, causing the death of twigs and flower buds. It acts with such vigor that the affected parts have the appearance of being scorched. Other bacterial diseases cause black rot of cabbage and the destruction of carrots and other fresh vegetables, especially during shipment.

Size and Growth Rates. Measurements of large numbers of different kinds of bacteria show the average length to be such that about 10,000 to 25,000 individuals, if laid end to end would make a line one inch long. To make this statement more vivid, from 30 to 70 of such organisms would be required, if placed end to end, to extend across the thickness of one page of this book. The usual unit of measure with the microscope is the micron, represented by the Greek letter μ. The micron is 0.001 mm. or about 0.0025 in. Average rod-type bacteria are perhaps 2 μ long by 0.5 μ thick.

Not only are these organisms amazingly small but their reproductive rates are correspondingly rapid. Under suitable conditions of food, moisture, and temperature some bacteria are capable of dividing every 20 to 30 minutes and there are records of much shorter periods than these.

This means that if a single mature organism divides into two equal parts, each of these will have grown to maturity and will again be ready to divide in 20 minutes. At this rate at the end of an hour there would be eight bacteria descended from a single individual; at the end of two hours there would be 64; and in three hours, 512. Obviously, under natural conditions it seldom occurs that there are 500 times as many bacteria in any given locality as there were three hours earlier. Almost always a shortage of food supplies or of other necessities for continued rapid growth, together with harmful excretions from the bacteria themselves, restrict the reproductive rate after a brief period of time.

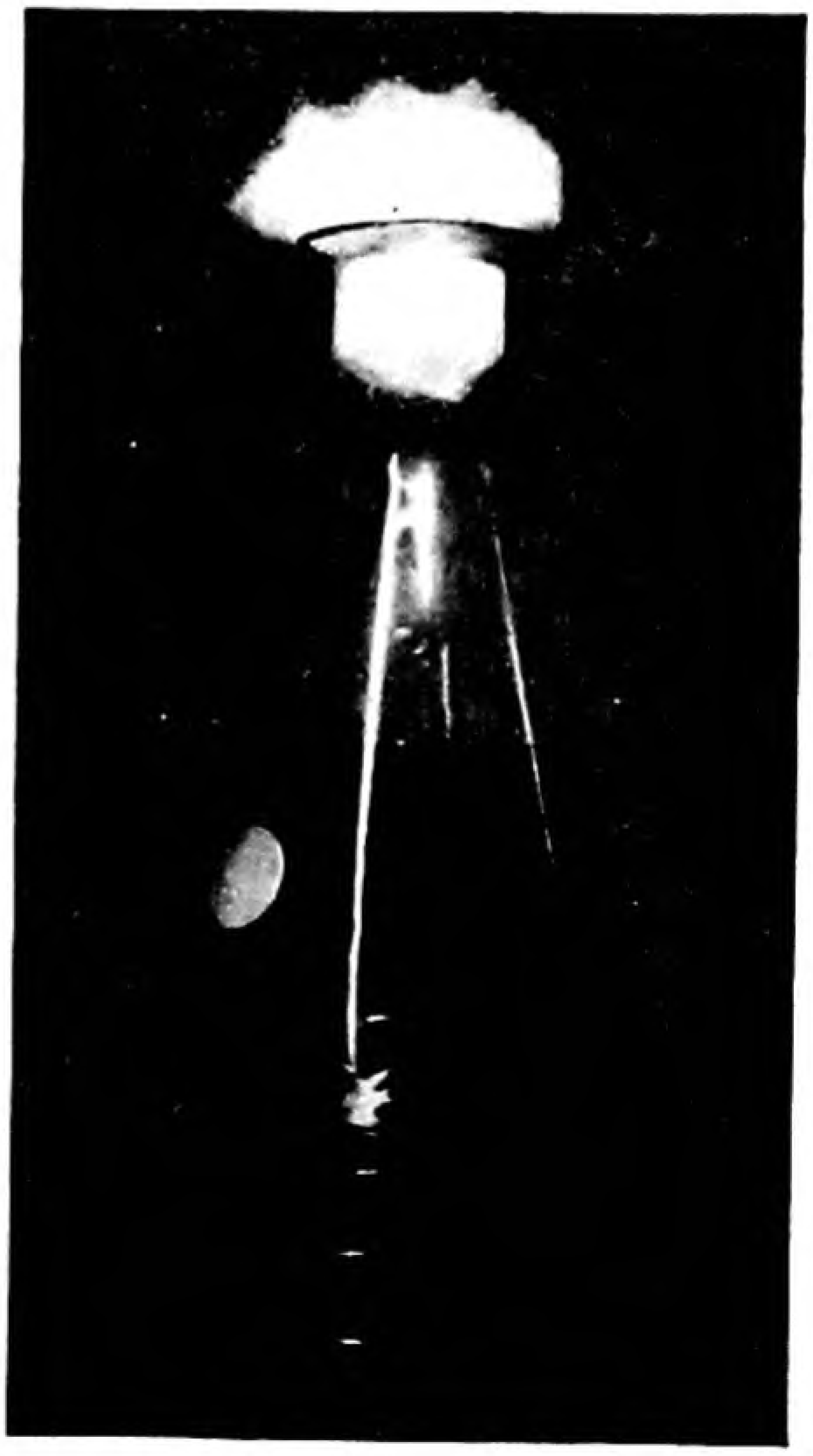
Methods of Studying Bacteria. DIRECT MICROSCOPIC EXAMINATION. In this day of good microscopes and wide acquaintance with bacteria it is relatively easy for any student to see these organisms. Nevertheless, because of their extremely small size, the beginner is almost always disappointed when he first attempts to examine them by this means.

Mixtures of many kinds of saprophytic bacteria can be seen with the microscope if water from a pond or ditch is placed in a vessel with decaying leaves or better still with a considerable mass of algae. Within a few days a scum forms over the surface of the water. While there may be primitive animals in this scum there are certain to be myriads of bacteria, so small that they appear to be only dancing points of light as seen with a high power of the microscope, that is, with a magnification of from 352× to 440×. A few of the larger species, however, can be seen fairly well with this magnification. In such a mixture the three forms mentioned above—rods, spirals, and spheres—can usually be recognized. Some of these appear as isolated cells and others are joined into short chains or grouped into colonies of various shapes; some swim about and others remain quiet; all appear to be almost transparent.

Since there is so little to be learned by a microscopic examination of bacteria, it may seem surprising that it has been possible to make the great progress that has been made in bacteriology. While the microscope is a necessary part of the equipment of the bacteriologist a number of methods of studying bacteria have been devised, each of which contributes greatly to an understanding of these organisms. Some of these methods follow.

CULTURING, ISOLATING, AND COUNTING. In most instances it is difficult to study bacteria in the places in which they grow naturally. The substratum or host may interfere with microscopic examination, and so many factors are out of control that experiments cannot be made satisfactorily. To overcome these difficulties the bacteria are grown on artificial media made of such substances as milk, specially prepared broths, gelatin and agar-agar. Each of these is useful for a limited number of purposes.

Agar-agar is employed to make a jelly-like colloidal foundation on which to grow bacteria. This substance cannot be digested by most species, and it is necessary therefore to add proper nutrients for the growth of the organisms being studied. The formula frequently used calls for 1.5 to 2 per cent of dry agar-agar in water with the addition of such



Agar-agar in flask stoppered with cottom plug to prevent entrance of bacteria.

bacterial foods as peptone (which is a mixture of amino acids and other substances from the partial digestion of proteins) and beef extract.

The agar-agar is boiled with the water. Then the entire mixture, including the nutrients, is sterilized by heating under pressure in an autoclave. The autoclave is practically the same as a pressure cooker. Sterilization usually requires a pressure of 15 pounds maintained for 15 minutes.

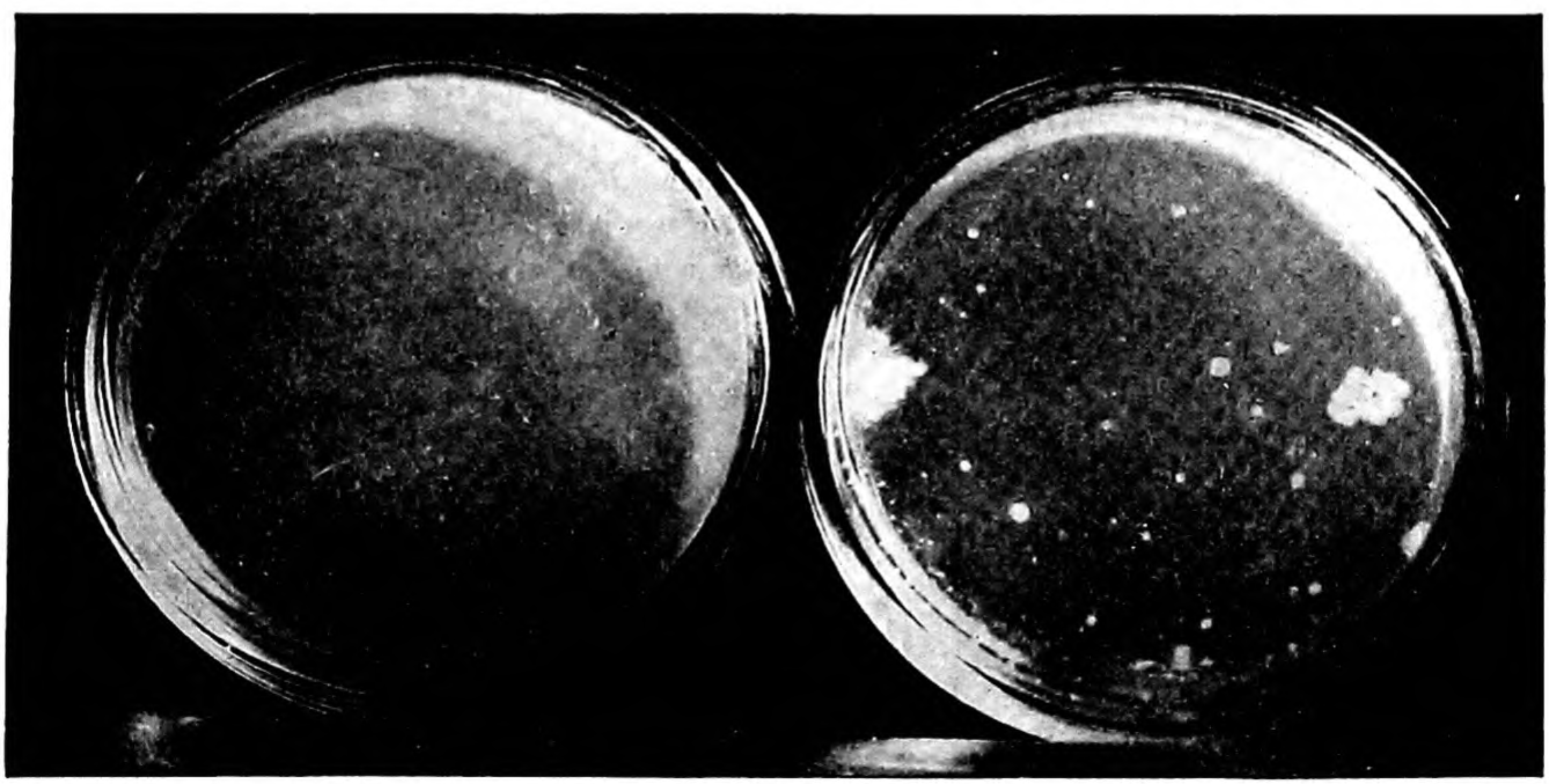
Some means must be used to prevent contamination of this sterile medium with bacteria from the air or other sources. To this end a plug of dry cotton is usually placed in the mouth of the flask in which the mixture is to be sterilized, before it is placed in the autoclave. This acts as an air filter through which bacteria cannot pass. As soon as the mixture is cool it takes the form of a firm jelly that can be used in a variety of ways, a few of which are described below.

In the early days of bacteriology various liquids were used as culture media. Since many kinds of bacteria usually grow mixed together it was difficult or even impossible to separate them for study. The discovery of solid culture media, however, solved the problem.

The following simple experiment illustrates the method: Warm nutrient agar-agar is poured into a sterile petri dish in sufficient amount to make a layer over the bottom. The dish is covered and cooled. After the culture medium has become firm it is ready to be used to grow bacteria. If the lid is removed for one minute numerous bacteria fall into the dish from the air. Then the lid is put in place again, preventing the entrance of other organisms. The petri dish is left in a warm incubator for 24 hours, whereupon numerous bacterial colonies can be seen without magnification. Each one of these colonies is made up of millions of cells, all descended from one individual. Under such ideal conditions many bacteria divide two or three times per hour. In 24 hours the numbers become almost unbelievable, and small as the individual cells are, the colonies are clearly visible.

Since all the cells of a single colony are directly related to one another, it is possible to establish a pure culture by the simple expedient of touching a sterile needle to a colony and transferring the organisms that cling to it to the agar in a sterile culture tube. When once isolated, a pure culture can be subjected to various kinds of experimental techniques.

By an adaptation of this method the bacteria in water, milk, or other liquids, can be either isolated or counted. Take milk, for example. To count the



Sterile agar-agar in petri dishes. (*Left*) Unexposed. (*Right*) Lid removed for one minute in a classroom. Both kept in warm incubator 24 hours.

bacterial cells in even a drop of the liquid would be impossible, but by means of measuring pipettes and flasks it is relatively easy to mix 1 milliliter (ml.) of milk with 99 ml. of sterile water (making a 1 : 100 dilution); or to make a 1 : 1000 dilution by adding 1 ml. of that mixture to 9 ml. of sterile water. By shaking these dilutions vigorously the individual bacterial cells are separated from each other and scattered throughout the liquid. If 1 ml. of the 1 : 1000 dilution is mixed with the sterile agar-agar in a petri dish, just before it is cool enough to solidify, and is incubated as usual, the colonies can be counted. Corrections are then made by multiplying the number of colonies by 1000, to indicate the number of bacteria in 1 ml. of the original milk. In badly contaminated milk much higher dilutions must be made, but the method of procedure is the same. It is possible to isolate a pure culture from any colony by the method described above whenever such isolation is needed.

For some purposes 10 to 12 per cent of gelatin is substituted for the agar-agar in making solid culture media. Either of these can be used in both counting and isolating bacteria from a mixture. Some kinds of bacteria digest gelatin, making a small liquid pocket around each colony while others do not. This difference helps in distinguishing species.

Culture tube containing an agar slant with bacteria growing on it.

Without solid media it would be all but impossible either to isolate pure cultures or to count bacteria. Nevertheless, various liquids give valuable information as to the effect of cultures upon the substances in which they grow. Certain species cause milk to curdle and others do not; some digest the curd after it has formed; and some produce acids or bases, which can be determined by means of litmus or other test materials.

Broth is used for several purposes, but one of the most important is to determine whether or not the bacteria being studied ferment certain sugars and produce such gases as carbon dioxide. To do this, *fermentation tubes* are filled with specially prepared broths, inoculated with bacteria and incubated. If gases are formed they collect in the closed arm where they can be measured and tested to discover their composition.

STAINING. Living bacteria are almost transparent and are difficult to examine with the microscope. But when they have been killed and stained they are much easier to see. In addition, many of the various stains used in microscopic work have a selective effect on bacteria, coloring some species and leaving others more or less unaffected. By testing mixed cultures it is often possible to identify certain of the species which are present. It is because of the positive identifications which can be made in this way that certain diseases, such as tuberculosis, have been so successfully brought under a measure of control.

Besides these various methods, the bacteriologist uses many others, all of which give information that can be pieced together either to identify the organisms or to disclose their physiologic activities.

Discovery and Growth of Knowledge of Bacteria. Bacteria are so small that their existence was unknown until Leeuwenhoek, a Dutch microscopist, made a microscope with which he could see them. In 1674 he first reported his strange dis-

coveries to the Royal Society of England. Bacteria, yeasts, and microscopic animals were seen, but their significance was in no way understood. Instead, for two centuries they were considered to be interesting, but unimportant playthings.

Then, with the discoveries that were made by Pasteur in the third quarter of the nineteenth century, it was recognized that bacteria cause decay and disease. When these facts became well known and generally accepted a whole new branch of botany began to develop. Bacteriology has now become such a highly specialized subject that both the techniques and the equipment used have been largely invented for the single purpose of dealing with these organisms. The recent development of the electron microscope has made it possible actually to see details of bacterial structure and activities that were known previously only by inference, bringing new progress in the understanding and control of bacteria. A comparison of the highest possible magnification of a given organism as seen with a good optical microscope with that of an electron microscope makes obvious the new advantage. Without doubt this new instrument will continue to bring accelerated progress in the study and control of bacteria.

Importance of Bacteria in the World of Life. It is generally recognized that a considerable number of diseases of human beings as well as of plants and of the lower animals are caused by bacteria. It is only natural, therefore, to associate all bacteria with ill health. As a matter of fact, however, only a very small proportion of all the kinds known are responsible for harm to any organism. The vast majority play a part in the decay of organic materials already dead by secreting enzymes that disintegrate the various kinds of cell walls, proteins, and fats.

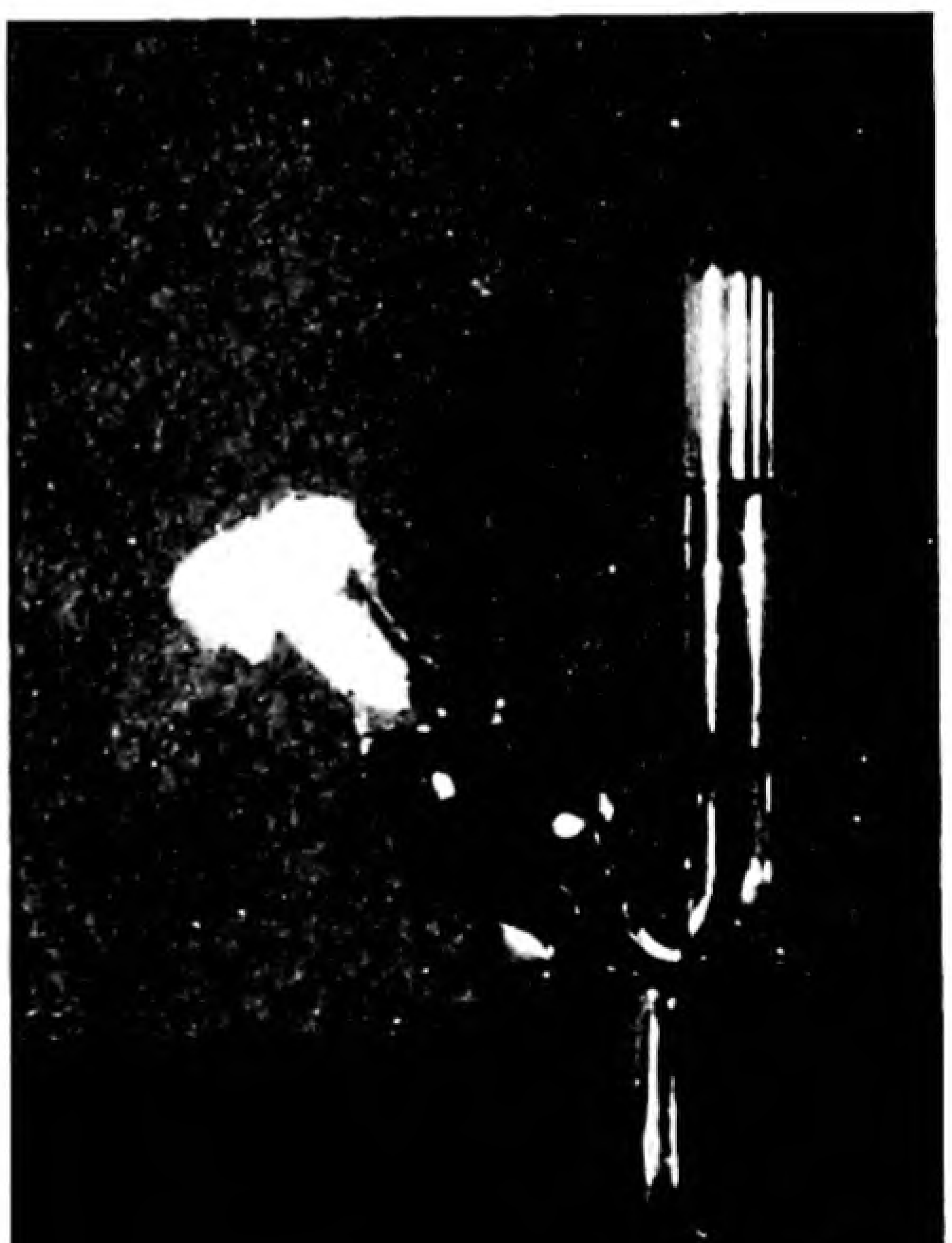
The destructive action of decay is important to higher plants and animals in many ways. First of all, it removes dead materials, leaving room for the living. Imagine the conditions that would exist in a forest, or grassland, or in the ocean, if throughout all time no leaf, tree trunk, algal cell, or animal carcass had ever disintegrated.

But decay does much more than merely provide room for the living. It changes complex organic compounds into the simpler forms which can be used by green plants. If bacterial decay did not occur, the life activities of plants and animals would of necessity come to a standstill because such cycles as those of carbon, nitrogen, and other nutrient elements would be retarded and finally brought to a full stop.

Without the carbon dioxide from the respiration of bacteria there would be so little in the air that photosynthesis would practically cease (see p. 22); and without the decay of proteins the nitrogen cycle would stop within a few years.

In the nitrogen cycle bacteria hold key positions in several places (see p. 59). The *nitrogen-fixing bacteria*, some of which grow in the soil and others in the root nodules of legumes, incorporate atmospheric nitrogen into their protoplasm. Eventually, this nitrogen appears in the form of nitrates in the soil. The green plant absorbs the nitrates and assimilates them, again organizing protoplasm. When death and decay come, *ammonifying bacteria* release ammonium, which is acted upon by two sets of *nitrifying bacteria*, forming first nitrites and then nitrates, thus completing a cycle.

Relationships of Bacteria. Bacteria are known to be an extremely ancient group because the ear-



Fermentation tube showing gas formation.

Photograph of *Mycobacterium tuberculosis*, the tubercle bacillus, taken with the electron microscope. Magnified to 21,000X. (Courtesy, Radio Corporation of America.)

liest fossils that have been discovered show a variety of evidences of bacterial action. In addition, some of the pre-Cambrian rocks almost certainly contain their fossilized cells. At present there is no evidence by which to decide whether blue-green algae or bacteria are more ancient. It is even possible that both of these were preceded by still more primitive and less well organized protoplasm, which may have been evolving for long periods of time before any of these organisms actually took form.

Although there is no direct and fully convincing proof by which to choose between them, three theories concerning the relationships between these two groups have been propounded.

The first of these is that bacteria and blue-green algae both originated from a still more primitive ancestor, each of these classes becoming specialized in its own way. This theory is based largely on logic. A second concept has been that bacteria originated from Cyanophyceae largely by the loss of the genetic capacity to produce chlorophyll. This theory is supported by the great similarities between the two in structure and reproduction. The remaining theory is that certain of the bacteria gave rise to blue-green algae. This idea is built on the fact that even today there are numerous kinds of *autotrophic* (*autos*, self; *trophikos*, feeding) bacteria that do not require organic materials as a source of food. Some of these utilize energy from the oxidation of sulfur, nitrogen, and other inorganic compounds.

There are several forms of sulfur bacteria, all of which are important from the standpoint of possible schizophyte relationships. These are often designated as the white, red, and green sulfur bacteria. There are several species of each.

Beggiatoa alba is a very common white form. This species often grows in water where hydrogen

sulfide (H_2S) is being set free, either from decaying organic matter or as a free gas in certain springs. Its respiration is strictly aerobic, that is, it uses free oxygen, as can be seen from the two equations below.

$$\underset{\text{Hydrogen sulfide}}{2H_2S} + O_2 \rightarrow 2H_2O + \underset{\text{Sulfur}}{2S}$$

The free sulfur remains in the cells and may be further oxidized as follows:

$$2S + 3O_2 + 2H_2O \rightarrow 2H_2SO_4$$

The sulfuric acid reacts with constituents of the soil, forming sulfates.

Both of these oxidations release energy that is used in the metabolism of the organism.

To grow *Beggiatoa* in the laboratory it is usually necessary only to place in a dish a small amount of soil from a pond or a poluted stream, with water shallow enough to permit oxygen to diffuse from the air through the water into the mud. To this is added a small pinch of sodium sulfide (Na_2S) every few days. As the organism grows it forms whitish patches on the soil or at the surface of the water.

Microscopic examination reveals threads of cells that have the appearance of diminutive colorless filaments of *Oscillatoria*. Even the swaying, rolling, and creeping motions of these plants are almost identical with those of *Oscillatoria*.

Most remarkable of all the known autotrophic bacteria are a few forms that have reddish or green pigments called respectively bacteriopurpurin and bacterioviridin. These pigments appear to be closely related chemically to chlorophyll. These forms are unable to grow in the presence of free oxygen, but are very common in anaerobic habitats. A peculiar kind of photosynthesis occurs in which carbohydrates are formed and sulfur, rather than oxygen, is the waste product.

These bacteria can be grown in the laboratory in exactly the same way as *Beggiatoa* except that the vessel in which they live must be kept in the light and must be filled completely with water and sealed or stoppered to prevent the entrance of oxygen.

The green autotrophs are very small spheres that cling together in chains, while the red forms are isolated rod-shaped cells that swim by means of flagella.

The white autotrophs are sometimes interpreted as the type of plant that may have given rise to such blue-green algae as *Oscillatoria*, and sometimes as its degenerate relatives. Likewise, the species which carry on photosynthesis have been thought to represent ancestral forms that had not yet evolved the efficient method of photosynthesizing which is made possible by chlorophyll.

These hypotheses lack confirmation, but this much seems certain: Organic compounds such as carbohydrates, fats, and proteins are unknown in nature except as they are produced by living things. It is almost certain, therefore, that the first feeble traces of slightly living material must have arisen from purely inorganic compounds and must have received from inorganic oxidations the necessary energy to permit a simple, primordial metabolism to occur at sufficient rates to maintain that spark of life.

Reasoning in this way certain botanists are inclined to suppose that some simple form closely related to autotrophic bacteria may have been ancestral to all other life, including blue-green algae.

SUPPLEMENTARY READINGS

Henrici and Ordal, "Biology of Bacteria."
Knaysi, "Elements of Bacterial Cytology."
Smith, "Fresh-water Algae of the United States."
Tilden, "Algae and Their Life Relations."

Chapter 14

RHODOPHYTA, PHAEOPHYTA, AND CHRYSOPHYTA

All plants that are more advanced than the Schizophyta have well organized nuclei. In addition to this mark of progress the red, brown, and golden algae have pigments in definite plastids. The following outline will summarize the similarities and differences among these groups.

	Pigments	*Food Reserves*	*Reproduction*
Cyanophyceae Blue-green Algae	Chlorophyll *a* Carotinoids Phycocyanin (sometimes phycoerythrin)	Glycogen or "animal starch," a polyglucose	Simple splitting of cells or fission; no sex.
Rhodophyta Red Algae	Chlorophyll *a* Carotinoids Phycoerythrin (sometimes phycocyanin)	"Floridian Starch," somewhat different from both glycogen and starch. Common sugars absent. Oil in some species.	Sexual reproduction rather complicated but without swimming gametes.
Phaeophyta Brown Algae	Chlorophyll *a* Carotinoids Fucoxanthin	Starch-like material but different from true starch. Oil in some species.	Zoospores and one or both gametes with laterally attached flagella. Sexual reproduction usual.
Chrysophyta Golden Algae	Carotinoids in large amounts Chlorophyll *a*, *b* Unidentified brown pigments	Oil is usual. Starch and starch-like substances in a few species.	Various. When cells have flagella they are lateral as in the brown algae.
Protochlorophyta and the higher plants	Chlorophyll *a*, *b*	Starch with some oils and fats. Also various sugars.	An extremely wide range from very simple to very complex.

Outline of the Chapter:
- Red Algae
  - *Batrachospermum*
  - *Polysiphonia*
- Brown Algae
  - *Fucus*
  - *Sargassum*
  - *Ectocarpus*
  - The Kelps
- Golden Algae
  - Diatoms
  - *Tribonema*

The red, brown, and golden algae are much more highly specialized than the blue-green algae, yet there is strong evidence that all these divisions of the plant kingdom are distant relatives. Mutations and new gene groupings, bringing about important hereditary changes, might be expected down through the ages, causing considerable diversity to occur. On the other hand, it would be surprising to discover that groups of somewhat similar plants were in no way related to each other. Using this criterion, we find a considerable number of similarities between the Rhodophyta and the Cyanophyceae. Hence these two groups may be properly placed together as probable relatives.

In addition to the carotinoid pigments which are always associated with chlorophyll, the red algae have a reddish coloring matter called *phycoerythrin*. This is the same, or almost the same, substance as the red pigment mentioned in the last chapter as being found sometimes, along with phycocyanin, in the blue-green algae. Likewise, in some or possibly all red algae, phycocyanin, the blue pigment of Cyanophyceae is formed, but in much smaller amounts. Conceivably such a coincidence of practical identity of at least four coloring materials could occur in two groups of plants which are in no way related to each other, but the more probable explanation would seem to be that each received from the same ancestors the proper sets of gene combinations to cause them to produce these four complex chemical substances.

One other characteristic possibly indicating relationship between red and blue-green algae is the complete absence of swimming cells of any kind in either group. In other words, these plants or their parts float in water and are carried aimlessly about, but none of them has any means of moving from place to place by flagella or other similar organs of propulsion.

On the other hand, the Rhodophyta are far in advance of the Cyanophyceae in several ways. In contrast with the poorly organized cells of the blue-green algae, those of the red algae have definite nuclei surrounded by nuclear membranes; and instead of the various color pigments being simply in solution as in the Cyanophyceae, they are organized into definite bodies, the *chromatophores*. And in one other fundamental way the red algae show a very remarkable advance over the blue-green algae. They have a complicated type of sexual reproduction. The evidence seems strong, therefore, that the red algae have evolved from the Cyanophyceae, following a course of development quite different from that of any other algal group.

Relationships of the Phaeophyta and Chrysophyta will be discussed in a later part of this chapter in connection with a somewhat detailed study of a few representatives of each of these divisions.

RED ALGAE

Almost all of the great group known as red algae or *Rhodophyta* (*rhodon*, rose) are marine plants growing attached to rocks at various depths along the sea coasts. They are a characteristic part of the flora of the warmer portions of the oceans just as the brown algae are of the cooler regions. There are some hundreds of genera of these plants. All are relatively small and delicate in appearance. Most species grow to be only a few inches long, although some reach a length of five or six feet. A few species thrive in streams of fresh water far inland.

As in other cases the common name of the group is only partly correct, for many species appear somewhat brownish, bluish, or olive green, depending on the relative amounts of the various pigments. The brightest colors occur in species that live in deep water and the dull ones are in shallow tide pools. In many of the Rhodophyta it is possible to see large protoplasmic connections between adjacent cells. When mitotic division takes place the new wall fails to close completely between the daughter cells, leaving protoplasmic strands uniting them.

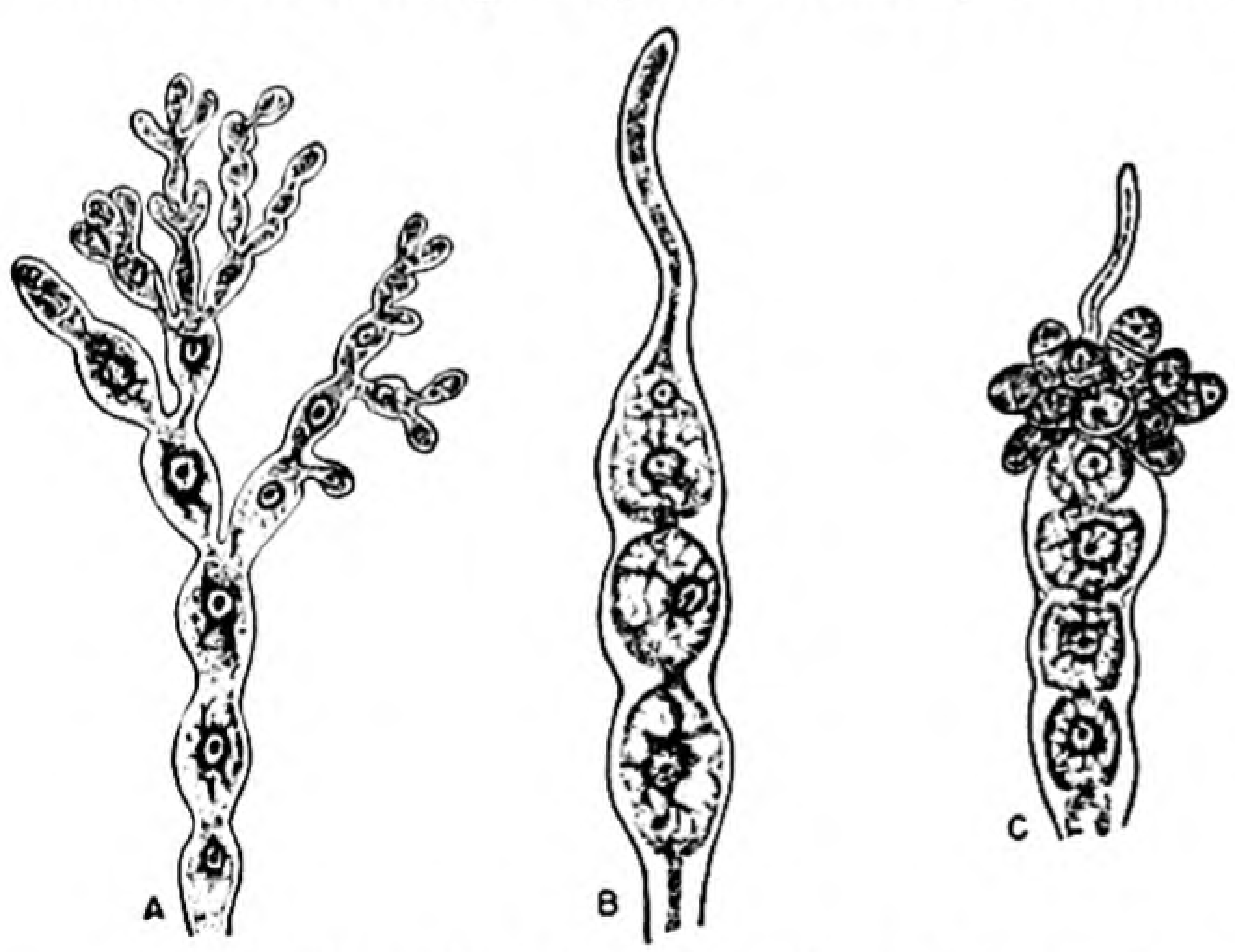
While we in the United States are just learning to make use of the red algae along our shores for food and in commerce, in some parts of the world, especially in the Orient, these algae are used for numerous products.

In discussing bacteria reference was made to agar-agar as a jelly-like medium that is much used in the growth of these organisms. This substance is made from several species of red algae, mostly belonging to the genus *Gelidium*, that grow attached to rocks in water some 50 feet deep along

the warmer coasts of both sides of the Pacific Ocean. Boat loads of these algae are collected by divers. On shore the plants are sorted, cleaned, and partly dried. The jelly is then extracted by steaming or boiling, after which it is poured off from the algal mass, and cleared either in settling tanks or by filtering. After it has cooled and solidified it is cut into bars or strips and dried ready for market. By far the greatest amount of the agar of commerce is prepared in Japan, although the industry is now growing on the west coast of the United States.

Agar-agar has numerous uses other than that of a culture medium for bacteria. In the Orient, soups, desserts, and other foods are made from it and it is used to stiffen silks and clarify beverages. In the United States it is used in jellies, ice cream, and candy, and as a sizing material for cloth.

At a few places along the Atlantic coasts another member of the red algae, the so-called Irish moss, *Chondrus crispus*, is collected in commercial quantities. This alga yields a jelly-like substance which enters into the composition of such widely varied products as shoe polish, paint, cosmetics, calcimine, and shaving soap. In addition, it is used



Nemalion. (A) Plant with Antheridia, each containing a sperm. (B) Trichogyne on young oögonium, ready to receive sperm. (C) Carpospores forming from the oögonium on the tip of a branch.

locally in the preparation of a number of desserts and other foods.

Batrachospermum. The genus *Batrachospermum* and its marine relative, *Nemalion* are good illustrations of the simpler red algae. Since the two are much alike, the fresh water form, which is probably available to a majority of students, will be described. The life history of Nemalion is almost identical with that of *Batrachospermum*.

ORGANIZATION. The *Batrachospermum* plant (*batrachos*, a frog; *sperma*, seed) is a small delicate branched filament a few inches long. It grows attached to rocks or other solid objects in shaded places in fresh water springs, lakes, and streams and in peat bogs in both Europe and North America. It is most luxuriant in early spring when the water is cold. The resemblance of its filaments to masses of frog eggs has given the plant its name. This appearance results from the fact that the plant body is made up of a group of slender, slimy branches. Whorls of very numerous small branchlets occur at frequent intervals throughout the length of these. It is this succession of compact whorls of grayish, greenish or purplish branchlets that gives to the plant the appearance of a string of beads or of amphibian eggs.

Growth of the larger branches of the plant occurs at their tips. At each tip is a single cell, called the apical cell, that divides mitotically and produces a succession of nodes with their whorls of short branches, and internodes which elongate, separating the nodes. Older portions of the axis are covered with a false cortex made of filaments which have grown down from a node above.

REPRODUCTION. Many years ago, when the life histories of the various groups of plants were not so well correlated as they are at present, students of the red algae had a special set of terms for almost all the structures concerned in reproduction. Now, however, since the relationships of the different parts of the plant kingdom are better understood, it seems best to use, as far as possible, the same terms as are employed in discussing the other algae.

The male gametes, or sperms, are formed in *antheridia*, and the eggs develop in *oögonia*. The antheridia and oögonia of *Batrachospermum* are borne on separate plants; that is, this genus is dioecious. These sex organs form at the ends of some of the branchlets. Each antheridium produces one sperm. When mature, a sperm simply escapes and drifts in the water, having no flagella or other

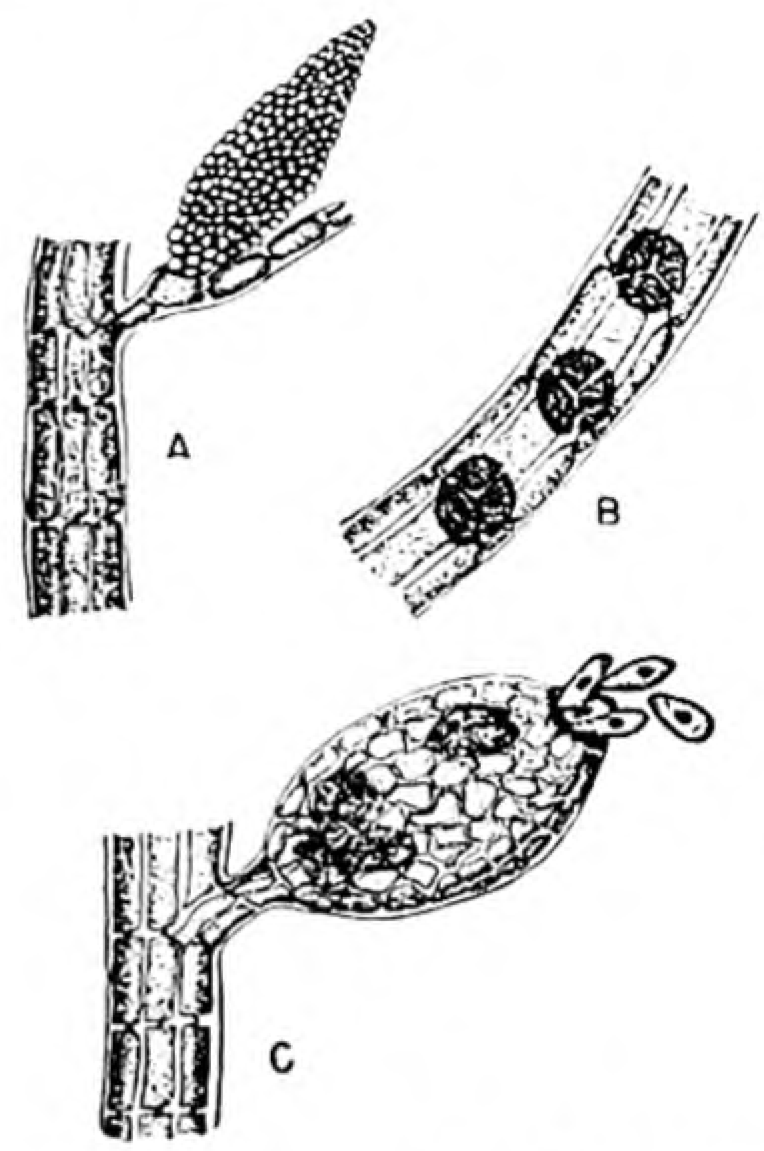
mechanism for swimming. Although mere chance movements of sperms as they are carried about in the water constitute a very uncertain method of reaching the egg, such large numbers are formed that it is doubtful if eggs are often left unfertilized.

The oögonium, often called the *carpogonium* (Greek *karpos*, fruit; *gonos*, offspring), is a peculiar structure with an enlarged basal part containing the portion of the protoplasm which is to function as the egg, and an elongated upper part, called the *trichogyne*. The wall of the trichogyne is gelatinous, and therefore floating sperms readily become attached to it. The protoplast of one sperm passes through the wall of the trichogyne, along its tube-like length, and into the oögonium where the nucleus unites with the egg, making the zygote.

Very soon after fertilization the zygote divides meiotically, producing two haploid nuclei. At about the same time a branch grows out from the base of what was the oögonium, and one of these nuclei migrates into it. The remaining nucleus divides again and again. At each division one of the daughter nuclei enters a newly formed branch. These branches together constitute the *cystocarp*. Each filament of the cystocarp cuts off a *carpospore* at its outer end. When the carpospore germinates it produces first a small, branched, filamentous structure which resembles some of the green algae. This is a juvenile form of the plant, and the adult individuals develop from it as a series of outgrowths.

From the best evidence, it seems that the main plant of *Batrachospermum* is in the haploid condition. In other words it is a gametophyte (see p. 156). The diploid portion of the life history begins with the union of the egg and the sperm and ends with the meiotic division when the fertilized egg begins growth. That is to say, the zygote is the only cell that belongs to the sporophyte generation.

Polysiphonia. This is a genus of strictly marine plants that is especially well represented along the shores of the Atlantic Ocean. These plants attach themselves to rocks, large algae and other supports, and grow to be a few inches long. Their colors range from pink and yellow to red, purple, brownish or almost black. *Polysiphonia* contrasts with *Batrachospermum* and *Namalion* in that it has an alternation of independent sporophyte and gametophyte generations. It takes its name (*polys*, many; *siphon*, a tube) from the fact that the plant body is constructed of several series of parallel tube-like cells that extend lengthwise, forming stem and branches.



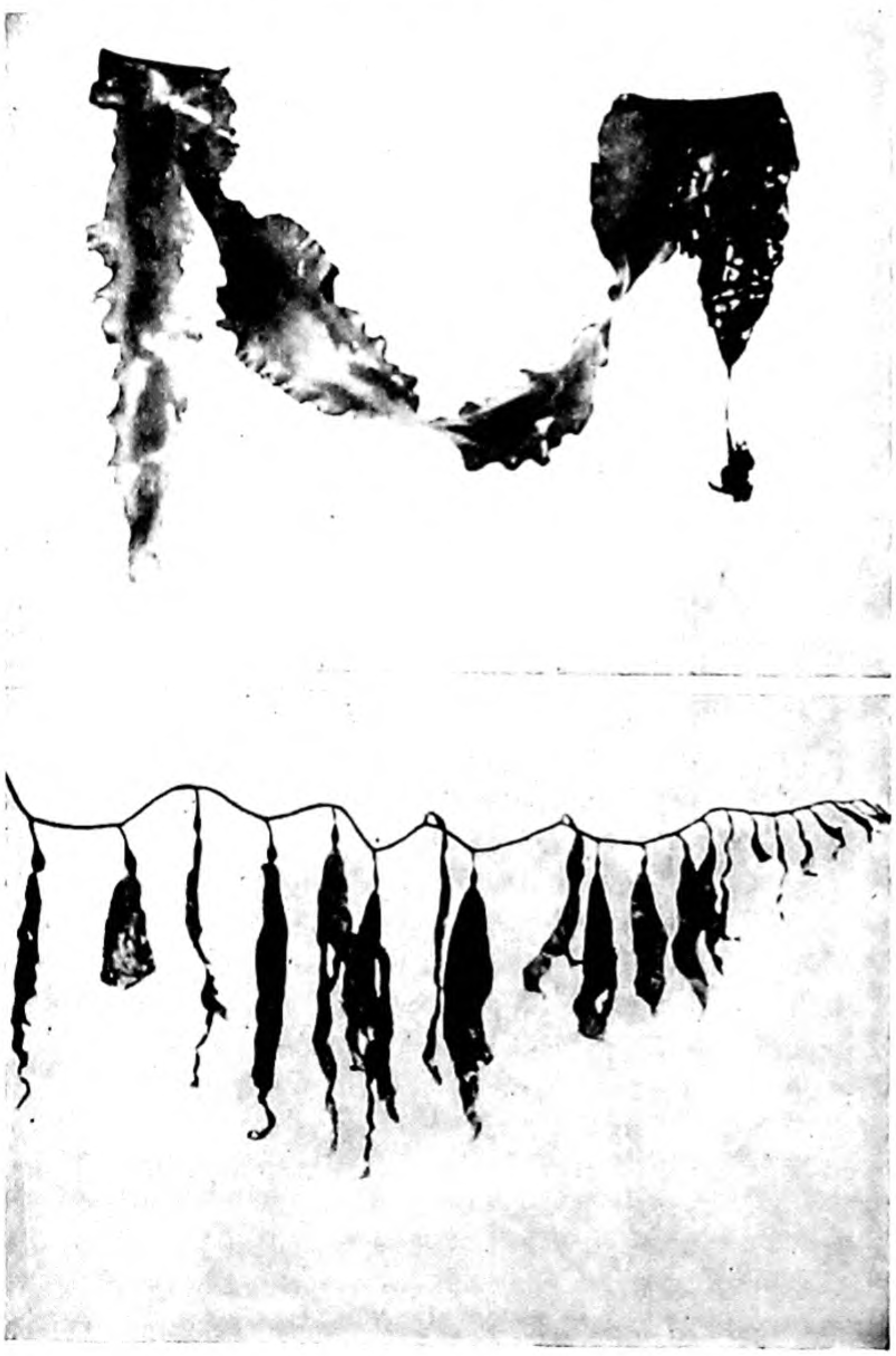
Polysiphonia. (A) Branch with cluster of antheridia. (B) Tetrasporic plant with three tetrads of tetraspores. (C) Cystocarp with carpospores escaping from sterile jacket.

Essentially, the antheridia and oögonia are much like those of *Batrachospermum*. The fertilized egg begins to develop branches as in that genus, and at the same time the cells below the oögonium put out a loose bell-shaped jacket of cells which surrounds the oögonium and its branches. This entire structure, although somewhat more complicated than that of *Batrachospermum* is called the *cystocarp*.

Carpospores are produced as in *Batrachospermum*, except that reduction division does not take place at this stage in the life cycle of *Polysiphonia*. Therefore, these carpospores are diploid. The carpospore grows into a diploid plant that has the same appearance as those which developed the oögonia and antheridia, but by meiotic divisions it produces haploid spores, the *tetraspores*, in groups of four. The tetraspores give rise to the haploid plants on which antheridia and oögonia are borne. Clearly, then, the male and female plants are gametophytes and the tetrasporic plants are sporophytes.

BROWN ALGAE

There is very little to indicate close relationship between the Phaeophyta and the other divisions of plants with the exception of the Chrysophyta, which will be discussed later. There appears to be no trace in the brown algae of the two pigments, phycocyanin and phycoerythrin, which are peculiar to the blue-green and red algae. Instead, besides the usual chlorophyll-carotinoid complex, characteristic of practically all plants which carry on photosynthesis, there is an additional carotinoid, called *fucoxanthin*. This pigment is of a rich golden brown color and is associated with the chlorophyll, carotin, and xanthophyll to form chromatophores. It would seem, however, that such invariable groupings of complex pigments as chlorophyll, carotin, and xanthophyll cannot be merely fortuitous accidents, but instead they strongly support the theory that all plants producing such a combination must be definitely descended from some common ancestral group from which they have inherited the capacity, or gene combination, which causes them to organize these particular substances. It might be argued that these pigments are in some way responses to light and the necessity for food, but the question may properly be asked how it could have happened that exactly the same means came into existence from unrelated sources.


Brown algae. (*Top*) *Laminaria* from Cape Cod. On the right may be seen large holdfast by which plant attaches itself to rocks. (*Bottom*) *Macrocystis* from southern California.

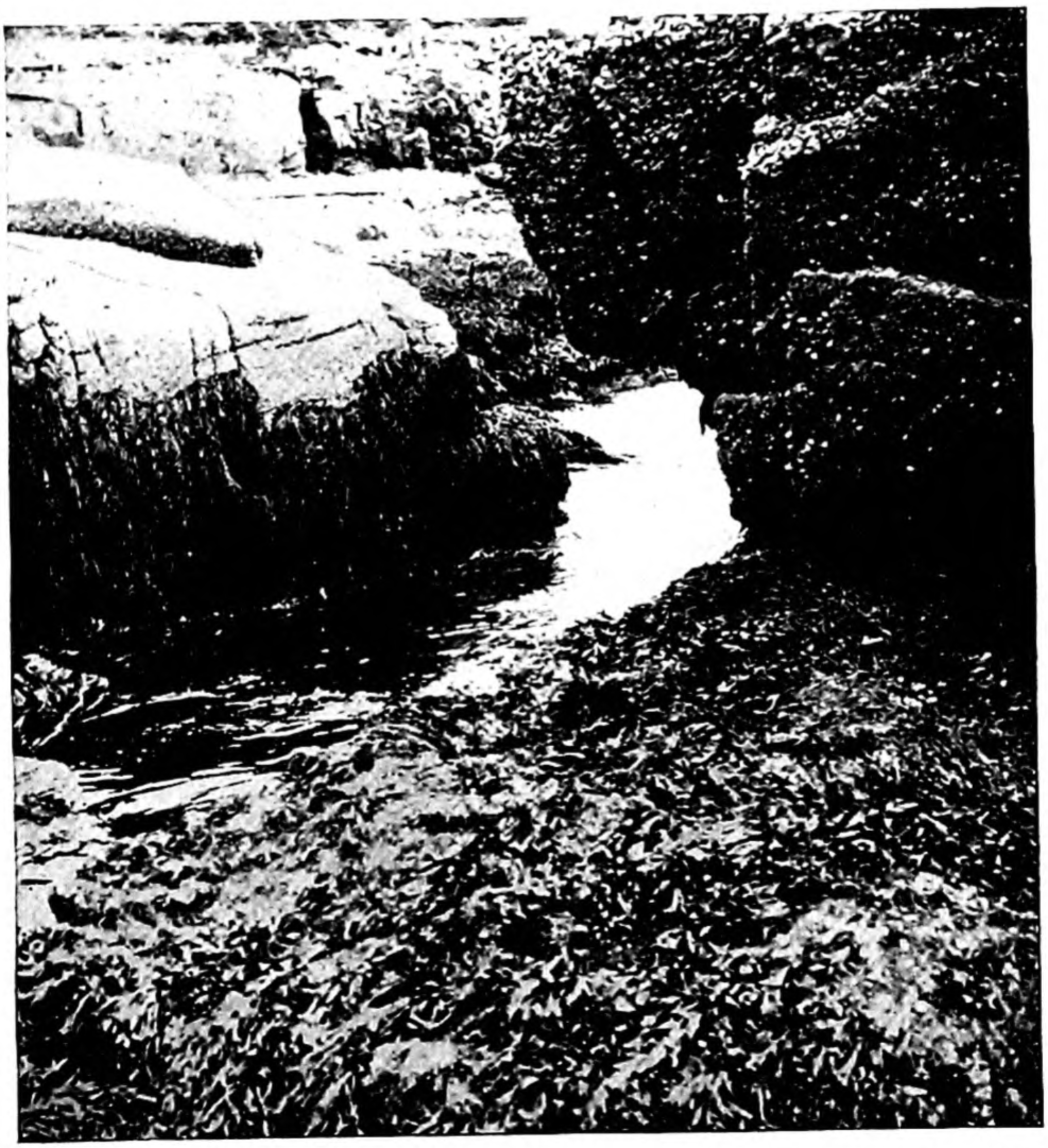
In contrast with Cyanophyceae and Rhodophyta, which have no swimming cells, many of the reproductive cells of the brown algae have *flagella* (*flagellum*, a whip). These are protoplasmic threads, by which the zoöspores and gametes propel themselves through the water. Each of these swimming cells has two, one long and one short, attached close together at one side of the cell. The longer points forward, while the shorter extends toward the rear.

The brown algae or *Phaeophyta* are so characteristically marine that the larger members of the group are commonly known as brown seaweeds. Although most of the largest of them grow in the cooler regions in water shallow enough for them to be attached, some live even in the tropical oceans and others are found floating in large quantities far from land and in warmer water. They range in size from small threadlike

forms to the giant kelps of the Pacific Ocean, which are sometimes more than a hundred feet long.

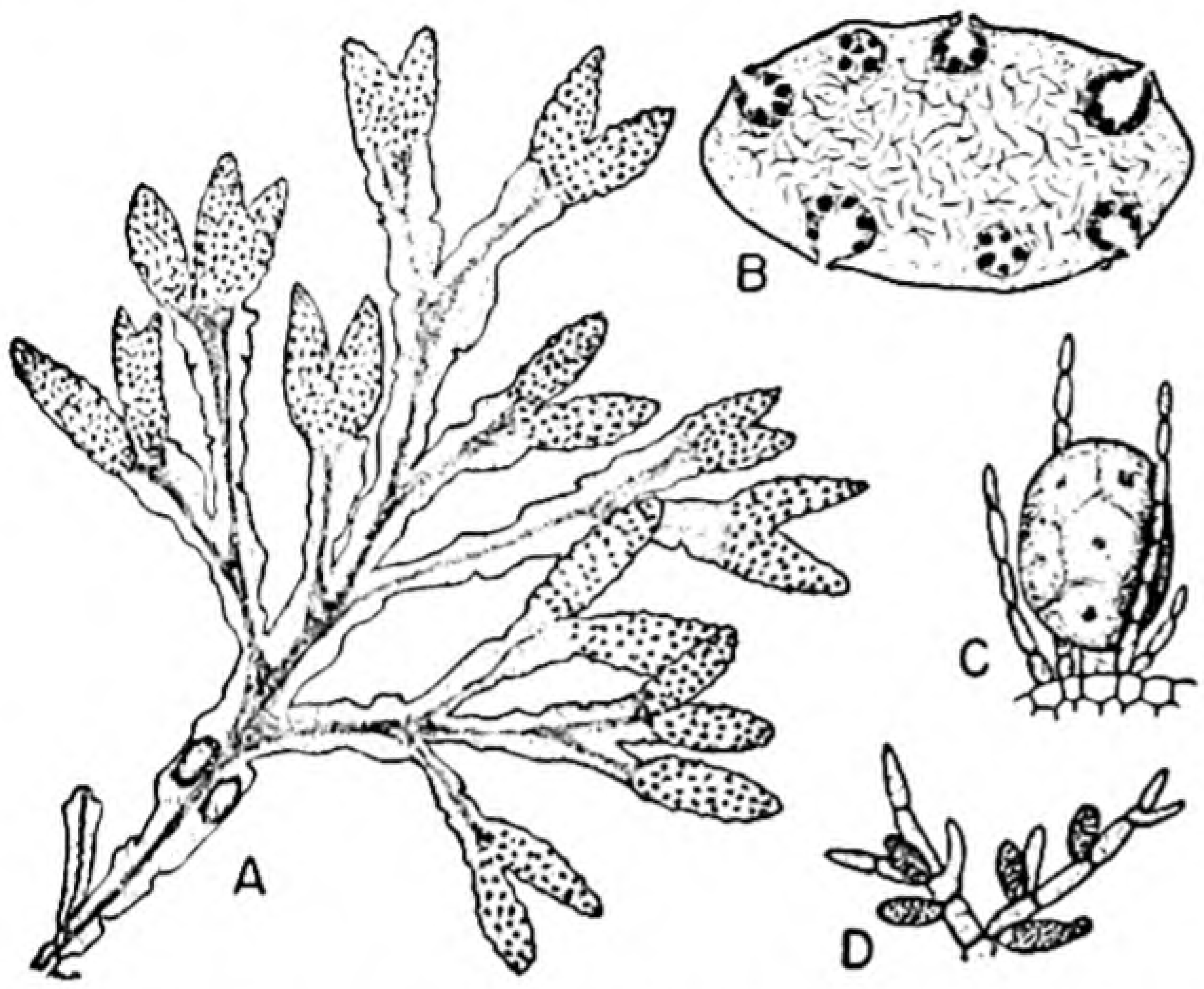
Fucus. Some of the most prominent brown seaweeds seen along the shore lines of the northern United States and Canada, as well as of northern Europe, are species of *Fucus* (*phykos*, a seaweed), often called rockweed. In contrast with most of the algae thus far considered, the *Fucus* plant is a comparatively wide, thick, rubbery thallus firmly attached to rocks or other solid objects by a cordlike basal holdfast. Its tough, leathery texture is well fitted to its habitat, for many species grow at the very edge of the water where they are subjected to severe wave action. In addition, they secrete large amounts of gelatinous material that spreads over them in the form of a slimy coat. This colloidal covering of the plant masses considerably restricts their rate of transpiration, for they are often exposed to the drying effects of the air for several hours daily while the tide is out.

STRUCTURE. The vegetative structure of the thallus is relatively highly specialized. Each branch grows by means of an *apical cell* located at the bottom of a small depression in the end. This apical cell is ancestral to all the other tissues, acting much like an apical meristem in a higher plant. In older parts of the thallus there is a sort of false epidermis and a cortex surrounding the pith. In certain species, large *air bladders*, located at various places on the plant, aid in holding it up when it is covered with water.



Fucus on sea coast while tide is out. (From Mavor: "General Biology." By permission of The Macmillan Company, publishers.)

REPRODUCTION. *Fucus* has no method of asexual reproduction. Pieces broken loose from their holdfasts may live for a time, but they have no way of attaching themselves again. New thalli sometimes grow out from old holdfast stumps from which the plants have broken away, but this can hardly be called reproduction.



Fucus. (A) Portion of plant. The small holes in the swollen tips of branches are the openings of the conceptacles; the two swollen places near base of plant are air bladders. (B) Section through conceptacles showing megasporangia (black spots) and threadlike paraphyses. (C) Megasporangium, showing six of the eight eggs, with four paraphyses. (D) Five microsporangia containing microspores.

The adult *Fucus* plant has the diploid number of chromosomes, and therefore is a sporophyte. The *sporangia* are borne in the tips of some of the branches of the thallus in special cavities known as *conceptacles.* These fruiting ends are larger and more rounded in outline than the ordinary vegetative tips, and the positions of the conceptacles are indicated externally by wartlike elevations, each with a small pore in its top.

The sporangia are of two kinds, *megasporangia* (*megas*, great) and *microsporangia* (*mikros*, small). In some species of *Fucus*, both form on the same plant, that is, the plant is *monoecious*, while in others they are separate, or the species is *dioecious*.

Within the conceptacles the sporangia are borne on short stalks attached to the walls. Associated with them are numerous hairlike filamentous branches, the *paraphyses* (singular, *paraphysis*). They probably have no function.

The first nuclear divisions in the developing megasporangium are meiotic, producing a tetrad of large *spores.* These divide mitotically, forming eight *eggs.* Therefore the gametophyte generation is limited to the two kinds of haploid cells: spores and gametes. A similar reduction takes place in the young microsporangium in which, however, 64 *sperms* usually organize.

Because of the peculiar sequence of events in the formation, first of spores and then of gametes within the same surrounding walls, there is much confusion in terminology at this point. With equal reason some persons call these containers *sporangia*, as has been done here, and others call them *gametangia* (*angeion*, a vessel).

The sperms are very active, each having two lateral flagella, but the eggs are large and have no means of moving about. They are released into the water where fertilization takes place.

One sperm unites with one egg, and the resulting zygote becomes attached to some solid object and grows directly into a new plant, the first mitotic divisions occurring within a few hours. Although dormancy at this step in the life cycle is advantageous to most algae, its absence is not a handicap to *Fucus.* In the environment in which it grows it can remain active in the vegetative condition throughout the year.

Sargassum. The genus, *Sargassum*, a near relative of *Fucus*, is mentioned because of its great abundance in some places.

In contrast with *Fucus*, however, this genus is indigenous to warmer parts of the ocean. *Sargassum* is especially abundant along the coasts of Australia and is to be found as far north as Japan, where some of the more tender plants are used for food. On the Atlantic side of the United States, gulfweed, as it is called here, is sometimes torn loose from its attachments by storms and carried in the ocean currents through the Gulf of Mexico, among the islands of the West Indies, and thence out to sea where it may float for long periods of time. Along the eastern coast of the United States certain species grow attached to rocky shores as far north as Massachusetts.

These plants have branched stems with flattened, leaflike outgrowths and stalked rounded air bladders that have much of the appearance of small cherries. When floating in water they resemble leafy branches of some woody plant with fruits attached.

Sargassum, showing resemblance to leafy stems, and berrylike floats.

The real fruiting tips, however, are much like those of *Fucus*, and the life cycles of the two are very similar.

Ectocarpus. This genus is represented by many species along sea coasts over the world. The plants usually grow attached to the larger, coarser seaweeds such as *Fucus* and the kelps, although occasionally they anchor to rocks or other nonliving objects.

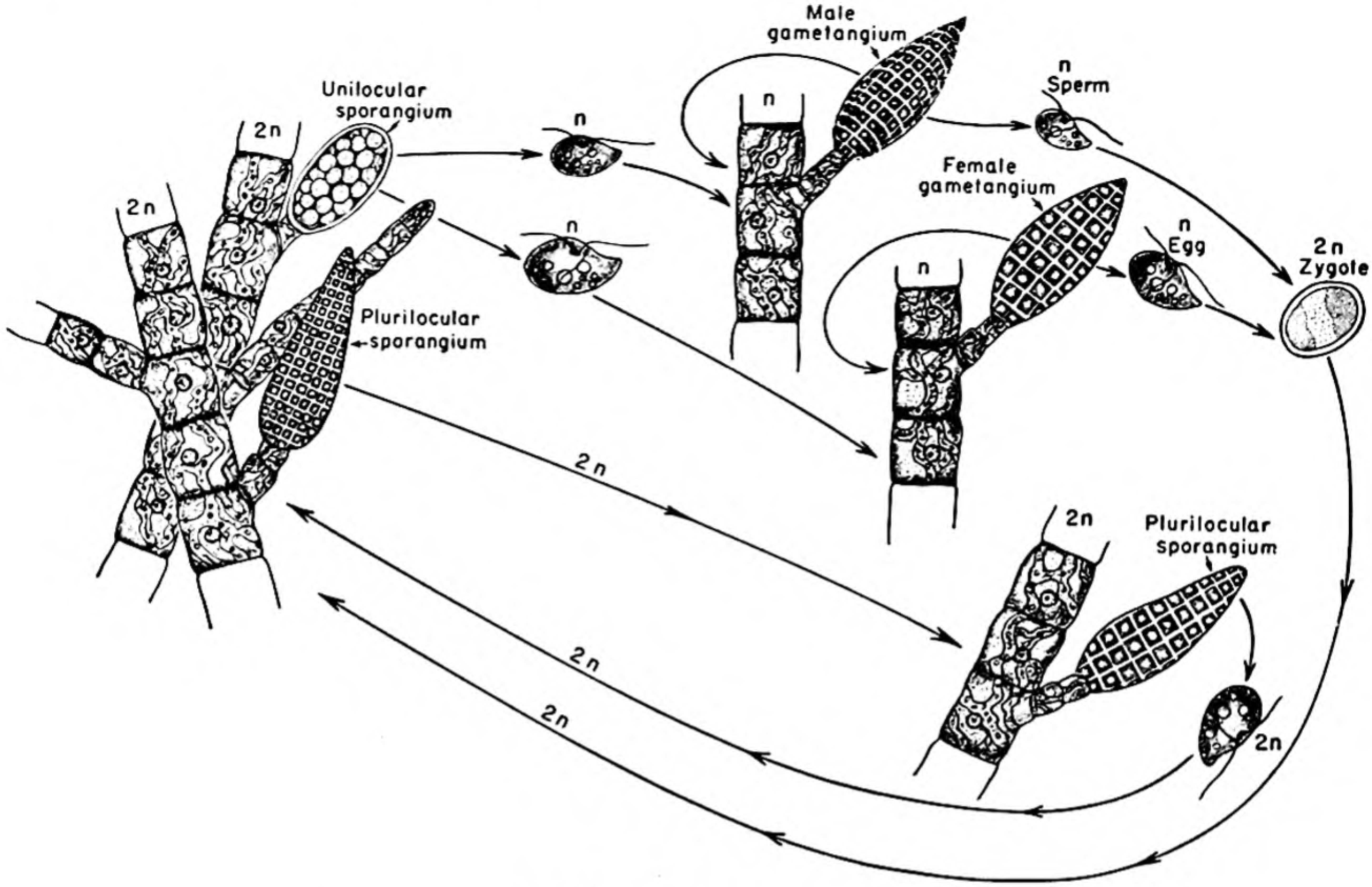
The plant body is composed of branched filaments up to five or six inches long. Each cell has a single nucleus and one or more simple or lobed plastids containing the usual chlorophyll-carotinoid pigments, and fucoxanthin, characteristic of the Phaeophyta.

The life cycle is somewhat complicated and confusing. In outline form, it is as follows: The zygote, as usual, is a diploid cell with which the sporophyte generation begins. It develops into the usual form of branched, filamentous plant which produces not one but two kinds of zoösporangia and zoöspores, or in other words, swimming spores. One form of sporangium originates as a single, enlarged, rounded cell at the end of a short branch (unilocular sporangium). The contents of this cell divide repeatedly, producing a large number of zoöspores. Reduction division takes place during this process; hence these zoöspores are gametophytic cells. When they grow they become gametophytes.

The other kind of zoöspores form in long, narrow, multicellular bodies (plurilocular sporangia), also at the tips of branches. These zoöspores are diploid and develop into other sporophytes similar to the one that produced them. The gametophytes that grow from the haploid zoöspores have exactly the same appearance as the sporophytes. Nevertheless, some of these gametophytes are males and others are females. The gametes which they produce appear to be almost identical but the ones from the male plants are actively attracted to those from the female plants. In other words, their behavior is that of sperms and eggs. But to complicate the situation, the gametes sometimes fail to fuse, and grow directly into other gametophytes.

In this life cycle there are three kinds of plants—male gametophytes, female gametophytes, and sporophytes—that have exactly the same appearance but which play distinct parts in the life history of the plant.

The Kelps. The word *kelp* is sometimes loosely applied to any of the coarser brown seaweeds, but it is most often restricted to certain large forms, such as *Laminaria* and *Macrocystis*. The kelps are great leathery plants and are the largest algae known, *Macrocystis* sometimes growing to a length of 150 feet. (See pp. 204 and 209.)



Life history of *Ectocarpus*.

Almost all members of this great group have powerful holdfasts that attach them to the rocks on the ocean floor, and flexible stems or stalks from which extend one or more long, broad, flattened blades.

The kelps live in water that ranges in temperature from cool to very cold, the distribution of some of them even extending far into the Arctic and Antarctic regions. The finest display in North America occurs along the Pacific coast from California to Alaska, where both the sizes and variety of forms are remarkable. Along the Atlantic coast there are considerable numbers of species and individuals, but few of them become more than three or four feet long, although occasional specimens have been reported to be as much as five or six times as large.

These giant algae form submarine fields or gardens at various depths from a few feet up to some 300 feet or more, depending on the clearness of the water and consequent penetration of sufficient light to permit efficient photosynthesis to take place. The blades of some of them float on the surface of the water while those of others are perpetually submerged.

At times of storms, kelps are sometimes thrown high on the beaches, forming windrows parallel with the shore line and occasionally extending for some miles, only to be devoured by insects and broken down by organisms of decay.

In the Orient the kelps are used in considerable amounts for human food. They are prepared as vegetables, relishes, soups, and beverages, and cooked with meats and fish. They are richly supplied with iodine, and consequently goiter is unknown among people who use them in large amounts in the diet.

An important industry is said to be developing around the harvesting, preparation, and transportation of the various products of these plants on both sides of the Pacific Ocean, but especially in the East. Until a few years ago the kelps were used as a commercial source of the two chemical elements, iodine and potassium. Of late, however, mineral

deposits have been discovered from which these products can be taken at less expense. Since potassium is deficient in many soils, kelps are often used as fertilizer near the sea coasts where they are plentiful.

As in *Fucus*, the large plant bodies of the kelps represent the sporophyte generation. At certain seasons of the year they produce numerous sporangia in clusters on the thallus. It was once thought that the zoöspores produced in these grew directly into new plants like those from which they came. It is now known, however, that in some species at least the spores have the reduced number of chromosomes and develop into microscopic filamentous individuals, the gametophytes, which produce gametes. The sperms and eggs unite, and new sporophyte plants result.

GOLDEN ALGAE

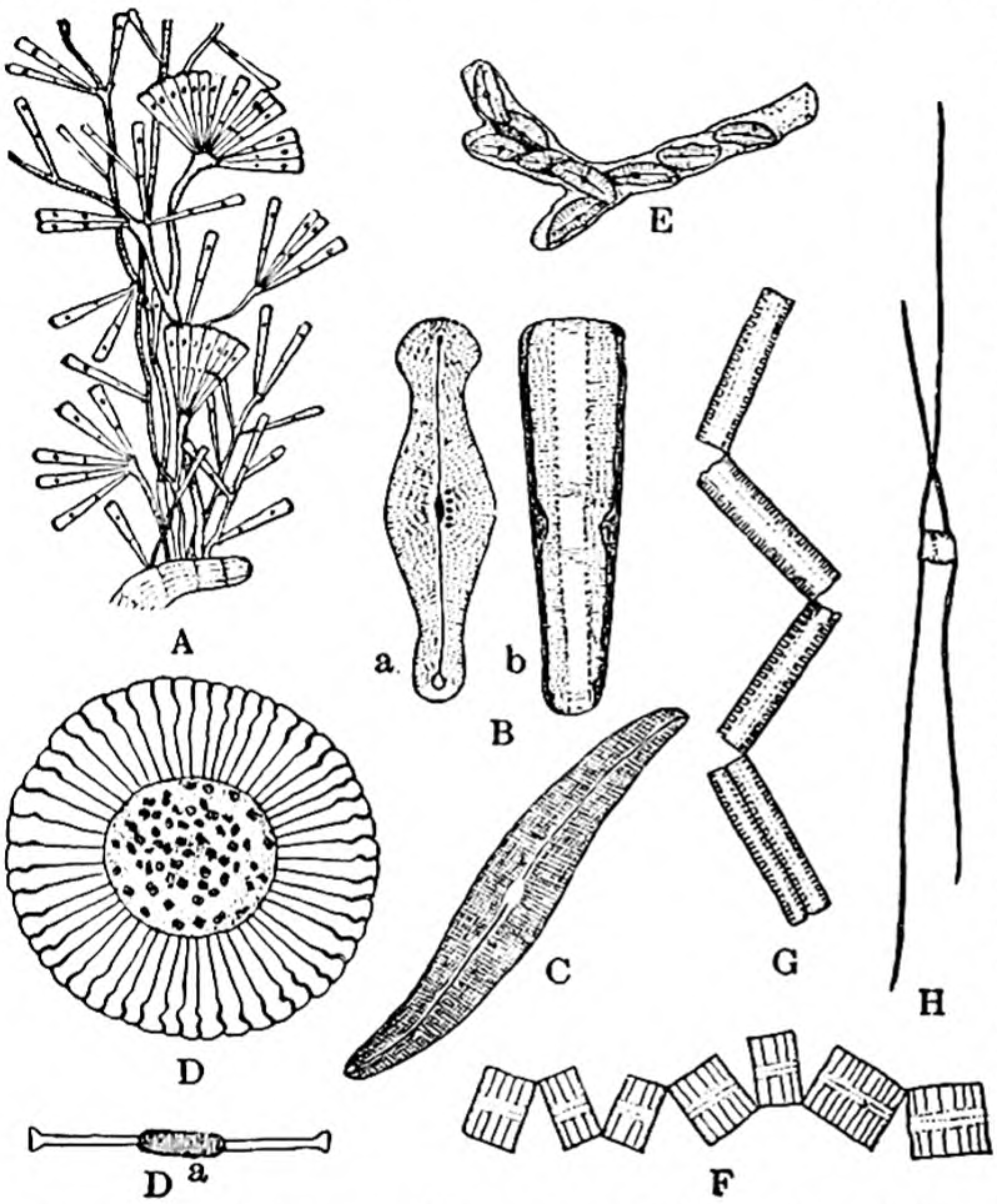
The Chrysophyta (*chrysos*, gold) constitute a peculiar assemblage of forms which assume many diverse shapes. Although these plants vary greatly in appearance, all have peculiarities which indicate a certain degree of natural relationship between them. Since this is a rather obscure group which is not often studied in great detail in general courses in botany this description will be limited to the diatoms and *Tribonema*.

The golden algae take both their English and technical names from the fact that the carotinoids are produced in much greater amounts than in the green algae. In addition, there are often brownish pigments. Such a combination gives a rich golden-brown color. In some members of this group certain of the reproductive cells have a pair of flagella of unequal length, suggesting a relationship with brown algae. Otherwise, relationships are uncertain.

Diatoms. These microscopic plants are among the most widespread of all algae. In fact they may be found in almost any natural water. They cling to vegetation in lakes and ponds; they form slimy coatings on stones or other supports in running water, often making olive-green or brownish masses, especially in spring and autumn; they grow scattered among other

Giant Kelps, showing stems, blades and floats. (Courtesy, Floyd Schmoe.)

algae; they are almost always to be found in laboratory aquaria; and throughout the surface waters of the oceans and along sea coasts they live in immense numbers.



Some typical diatoms. (A) *Licmophora flabellata* (Carm.) Ag. (B) *Gomphonema geminata* (Lyngh.) Ag; (a) valve view, (b) girdle view. (C) *Pleurosigma attenuatum* (Kütz.) Wm. Sm. (D) *Planktoniella sol* (Wallich.) Schütt.; (a) valve view. (E) *Cymbella caespitosa* Kütz. (F) *Tabellaria flocculosa* (Roth.) Kütz. (G) *Diatomum vulgare* DeBary. (H) *Chaetoceras boreale* Bail. (From Engler and Prantl. Courtesy, D. M. Mottier: "College Textbook of Botany," Philadelphia, The Blakiston Company.)

In the oceans they constitute the chief food for the myriads of minute Crustacea which, in turn, are eaten in great quantities by larger crustacean species and by small, young fish. Both of these become the food of somewhat larger fishes, thus starting a food chain which leads to the feeding of the largest animals of the sea and so, together with other algae, to eventuate in the major part of the seafood used by man.

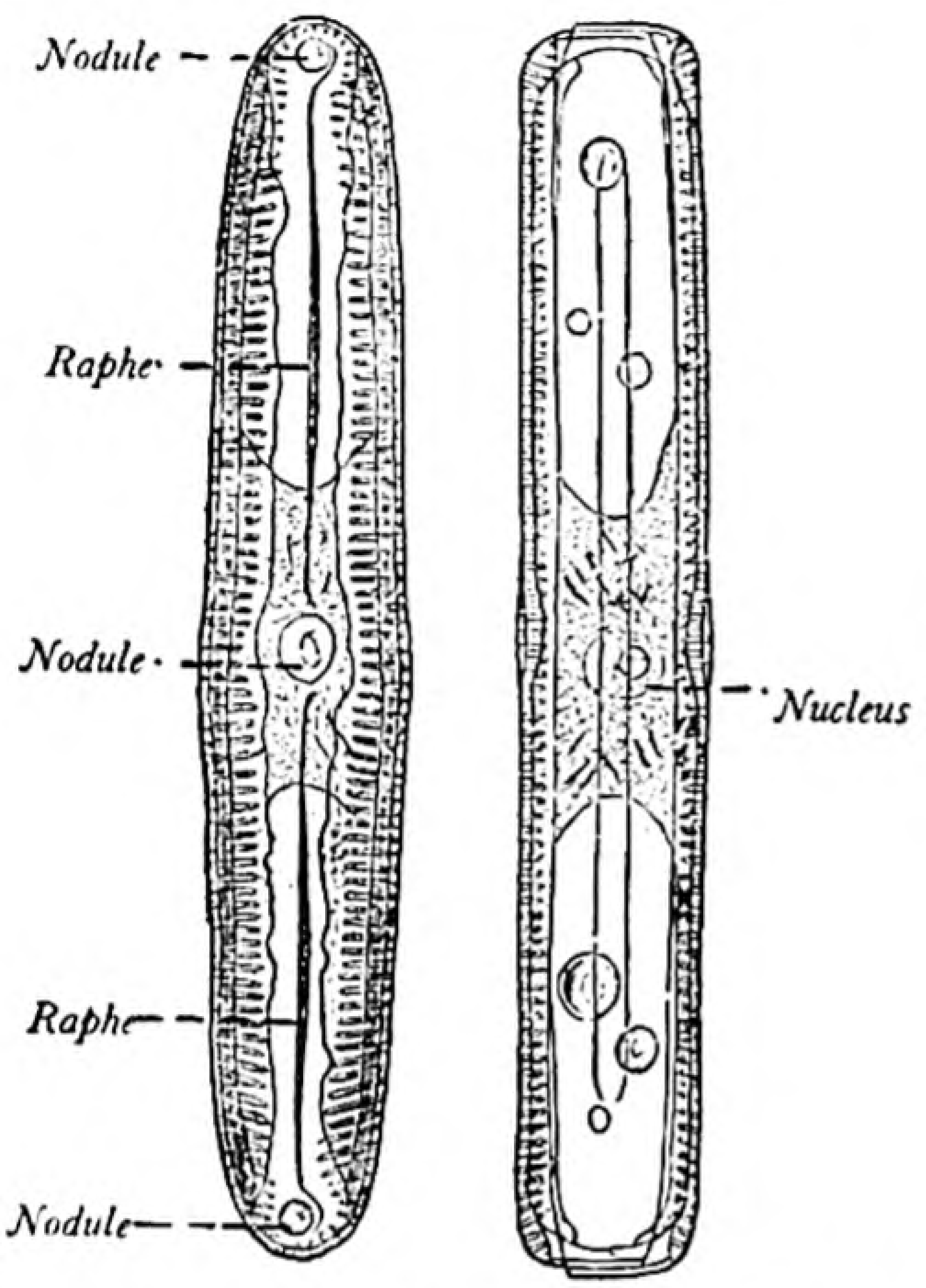
Diatoms are unicellular and usually are beautifully symmetrical. They take many forms, including circles, squares, triangles, boat shapes, and various types of curves. In some species they cling together in ribbonlike colonies and in others they are attached to objects by long, gelatinous stalks. Those which are not attached are often motile, and the diamond-shaped or boat-shaped forms following a jerky zigzag course across the field of view of the microscope are a familiar sight in almost every microscopic preparation of living algae. This motion is not brought about by the action of flagella. In fact, the mechanism involved is not fully understood.

Cell Structure. The most significant characteristic of the cell is the wall. It is a pectic compound reinforced with a deposit of silica, a substance much like glass. Many interesting features of the life of the organism are determined by the firm, unyielding nature of this enclosure. When the plant dies and decays, this glassy shell sinks to the bottom of the body of water and, being practically indestructible, remains there indefinitely. Deposits of "diatomaceous earth" are sometimes hundreds of feet thick and in one place a layer 3000 feet in thickness is known. These deposits are made up almost entirely of the tiny shells and are widely distributed in thicker or thinner layers over the earth's surface.

The glassy wall does not make a complete, impervious covering over the cell but is really in two parts, known as valves, which fit together like a box and its lid and, although the actual size of these does not change after they are once formed, the protoplast inside may enlarge and push them farther apart so that they do not overlap so far.

The valves of the various genera and species of diatoms are differently marked and ornamented but only a single species will be described here. *Pinnularia nobilis* is large and therefore easily studied and

it is widely distributed in fresh water in both North America and Europe. This diatom, in common with many others, appears very different as seen from various angles. The view from the side is called the *girdle view* while that looking down on the top of a



Two views of the diatom *Pinnularia*. (*Left*) Valve view. (*Right*) Girdle view, showing cell contents. (From Youngken. After Strasburger: "Text Book of Botany." By permission of The Macmillan Company, publishers.)

valve is the *valve view*. Along the center of the valve is to be seen a line, the *raphe*. This is a long slit in the wall. At its middle there is a circular *central nodule*. This is an internal thick place in the wall that interrupts the raphe. At each end of the wall there is also a *polar nodule*. Numerous heavy ridges in the walls, the *costae*, extend outward from the raphe in both directions. The girdle view shows the nodules and costae from a different angle as well as the relation of the *outer* and *inner valves*.

The cell has two flat plastids which stand on edge in the valves. These usually have a brown pigment, sometimes known as *diatomin*, which may be a carotinoid. This pigment often completely obscures the chlorophyll, giving the diatom its characteristic yellow or brown color. The nucleus is in the middle of the cell between the chromatophores.

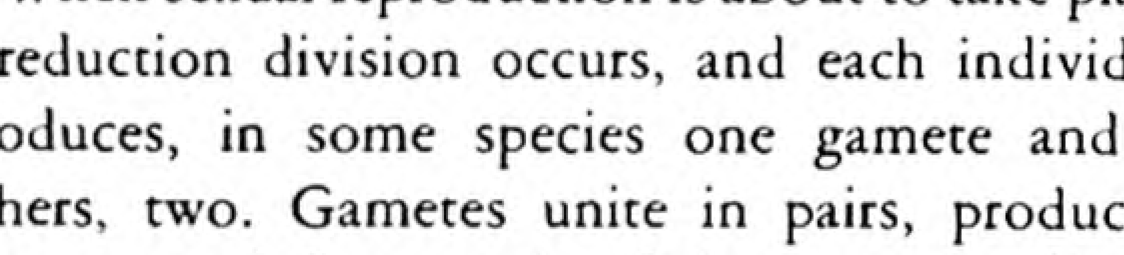
Reproduction. The common method of reproduction in most diatoms is cell division. The cell grows to the point where the outer valve is lifted almost off the box. Then mitotic division takes place and both chromatophores split lengthwise. To complete the process, each of the new protoplasts produces a new valve which fits inside the old one received from the parent.

A careful study of this kind of behavior will make it obvious that one of the new cells is of the same size as the parent, but the other, now using the old box as its lid, is slightly smaller. As division continues, a series of sizes of cells will be produced, and it is evident that a few of these protoplasts will be very small. These minute plants lose their walls and become *auxospores*, meaning literally, growing spores. Each of these may enlarge to its maximum size and then, by a more or less complex process, develop the usual type of shell.

When sexual reproduction is about to take place, a reduction division occurs, and each individual produces, in some species one gamete and in others, two. Gametes unite in pairs, producing zygotes, and from each of these a new diatom develops as an auxospore.

From this discussion it is evident that the diatom is diploid, corresponding to the sporophyte generation of other plants, and that the gametophyte is represented only by the gametes.

Tribonema. This genus represents a second class of the Chrysophyta, known as the Heterokontae. In general appearance it is much like an unbranched green alga. In usual laboratory work one may not discover its presence until the broken end of a filament is encountered. Here a narrow H shape of wall extends a half cell-length beyond



Tribonema showing the characteristic H-shaped cell walls.

the end of a filament. More careful searching is likely to disclose H shapes floating about where the walls have broken apart. These walls are formed one inside the other, somewhat after the manner of those of a diatom. The walls of *Tribonema* cells

are of pectic substance. Special treatments that cause pectin to swell show that it is formed in several layers. Reproduction occurs chiefly by means of isogametes and of zoöspores.

Summary. The three divisions of plants illustrated in this chapter may be treated as rather distant cousins, the blue-green algae or, perhaps their immediate forebears, being ancestral to all of them. If this interpretation is correct, each of these groups has followed its own peculiar lines of development and the hundreds of species of red, brown, and golden algae, known at the present time are the results of specialization and genetic divergences within these great divisions.

SUPPLEMENTARY READINGS

Arnold, "An Introduction to Paleobotany."
Fassett, "A Manual of Aquatic Plants."
Smith, "Fresh-Water Algae of the United States."
Tilden, "The Algae and Their Life Relations."

Chapter 15

PROTOCHLOROPHYTA: GREEN ALGAE

It is not known just where or when, or from what ancestors, the first green algae developed, but there is ample evidence that they are, geologically, a very ancient group of plants.

All have true chloroplasts that contain chlorophyll and the carotinoids in much the same proportion as they occur in modern higher plants. For this reason they have been called "grass-green algae."

Of the hundreds of genera that are included in the present-day green algae only a few of the commonest can be studied profitably in an elementary course of botany. Some are so rare, others so difficult to interpret, and still others are of such unusual nature, that they must be left to the more advanced student and to the specialist.

The following outline indicates the orders (omitting the families) into which the genera to be discussed here are grouped, and the sequence in which they are treated.

Orders
- *Genera*

Volvocales
- *Chlamydomonas*
- *Gonium*
- *Pandorina*
- *Volvox*

Euglenales
- *Euglena*

Ulotrichales
- *Ulothrix*
- *Coleochaete*
- *Protococcus*

Cladophorales
- *Cladophora*

Oedogoniales

Oedogonium

Orders
- *Genera*

Zygnematales
- *Spirogyra*
- *Zygnema*
- *Mougeotia*
- Desmids (a family)

Chlorococcales
- *Pediastrum*
- *Scenedesmus*
- *Hydrodictyon*

Siphonales
- *Vaucheria*

Charales
- *Chara*

General Considerations. The name Chlorophyta has sometimes been used as the technical name for the green algae, but since this word really means green plants (*chloros*, green; *phyton*, plant), it seems more suitable to use a more limited designation for the group. Because the green algae are primitive green plants and are sharply set off from other divisions by fairly definite characteristics, an appropriate name for the group is *Protochlorophyta* (*protos*, original or primitive).

Green algae are very widely distributed over the earth, but they are especially common in fresh water. Streams, lakes, and ponds, are almost always well populated by these plants. Some of them grow attached to sticks, stones or other objects in the water, and others are free-floating. Many species produce thick-walled zygotes or other specialized cells that endure hard conditions such as drying or cold. These cells are probably carried long distances in the wind, but an even more direct and

effective means of distribution results from the migration of waterfoul. The web-footed species, especially ducks and geese, carry considerable quantities of mud in the cups of their feet as they fly from place to place, distributing myriads of microscopic propagules. Such ready transfer doubtless accounts for the widespread distribution of many species of algae, some of which occur in suitable places over the entire Northern Hemisphere.

A few genera, such as sea lettuce, *Ulva*, and certain filamentous forms are common along sea coasts. Some species grow in the surface layers of soil, on the bark of trees, on shingle roofs and in other places where there is relatively little water.

These plants vary greatly in complexity. Many are one-celled forms, others are branched or unbranched filaments, and only a few exhibit more than very simple organization. All cells, however, have well-constructed nuclei.

The shapes of the chloroplasts vary considerably among the different genera. Some are much like those in the seed plants but others take the form of ribbons, cups, and bands, to mention only a few. Whatever their shape, however, all contain the chlorophyll-carotinoid complex that is characteristic of the higher, most advanced divisions of the plant kingdom.

The green algae have one other important similarity to higher plants: the usual reserve carbohydrate is starch. In a few species reserve food takes the form of oil, but even in these, long continued photosynthesis leads to starch production.

Aquatic green algae, in common with chlorophyll-bearing water plants of all classifications, play two important parts in the world of life. They furnish immense amounts of food for animals from protozoa to fish, and at the same time they release much of the oxygen that is used in the respiration of both plants and animals in the water.

When or from what group of ancient plants the green algae arose is unknown but it is evident that their ancestors had the ability to produce chlorophyll and the carotinoids and therefore to carry on photosynthesis. It seems entirely improbable that such gene combinations as are required to produce all the complicated compounds of the chlorophyll-carotinoid complex have originated more than once since life first appeared on earth. All chlorophyll-bearing plants, therefore, must have evolved directly or indirectly from some group which also had chlorophyll. So far as is known the most ancient of these are the Cyanophyceae. They may be the direct ancestors of the rest; or all, including the blue-green algae, may have evolved from a still more ancient form. Having arrived at the Protochlorophyta, however, the relationships of other green plants seem relatively clear. This statement will gradually take on meaning in later chapters.

For some reason the idea is prevalent that algae, especially those which form a scum on the water, are loathsome or filthy. This is far from the truth. In fact, many of the green algae are very sensitive to impurities in the water in which they grow and are quite as clean as fields of wheat, corn, or cane. Even a few minutes spent in examining some of them with the microscope does much to dispel the feeling that the algae are repulsive, and at this point the student may look forward to an entirely new field of intense fascination as he begins the study of these microscopic forms.

Because people in general are seldom interested in microscopic algae, few species, except the largest or those which grow in conspicuous masses, have any definite common names, and in discussing many of them it is necessary to use the technical names of genera or larger groups.

Volvocales. The order, *Volvocales*, includes all the green algae that swim by means of flagella in the adult stage. The members of other orders, and in fact of other divisions of the plant kingdom, may have similar cells in their reproductive stages, but never in the adult plants. The various species belonging to this order are widely distributed in stagnant fresh water that is rich in dissolved nutrients.

CHLAMYDOMONAS. The individual in this genus is always a single cell. There are about 150 species of *Chlamydomonas*, the majority of which have the characteristics described below. Each cell has two flagella located at its anterior end, contrasting in position with those of the swimming cells of both the brown and golden algae. Near the base of the flagella is an eyespot and at the opposite end of the

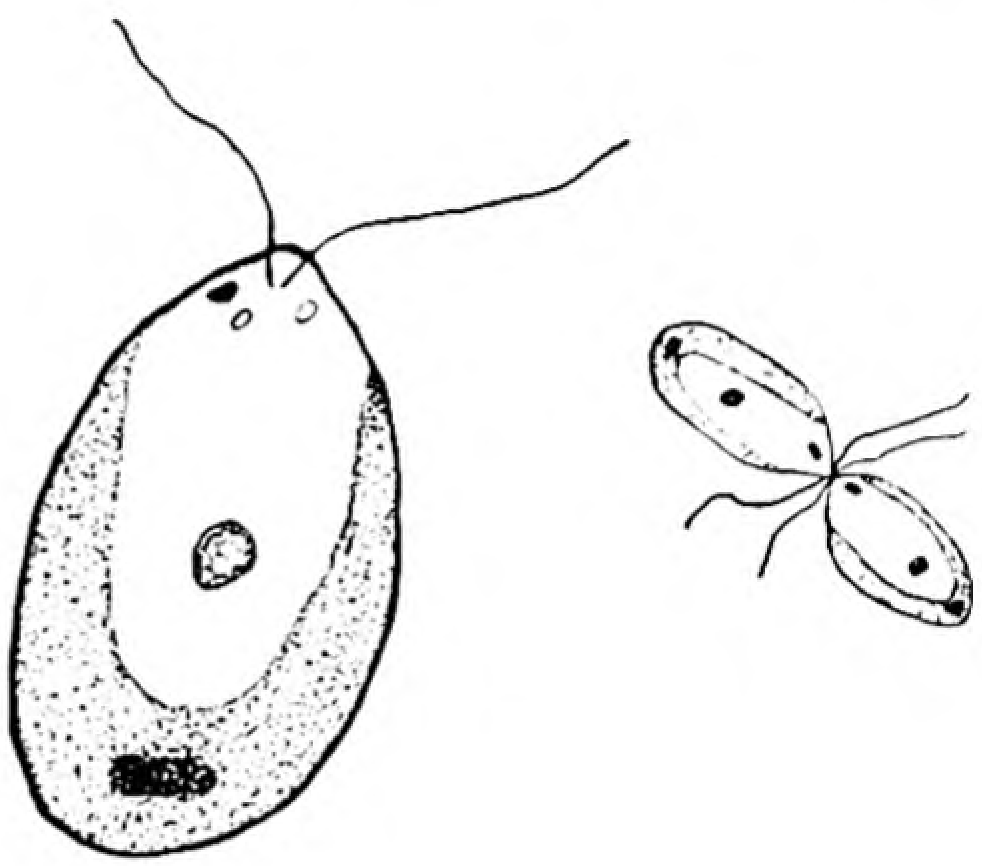
cell is a single chloroplast that usually takes the form of a cup, a part of which is a specialized protein body, called a *pyrenoid*. The nucleus occupies the bowl of the cup. Two small contractile vacuoles and a light-sensitive stigma colored reddish by a carotinoid are near the base of the flagella. These structures suggest a possible relationship to the Protozoa. The cell wall is of cellulose.

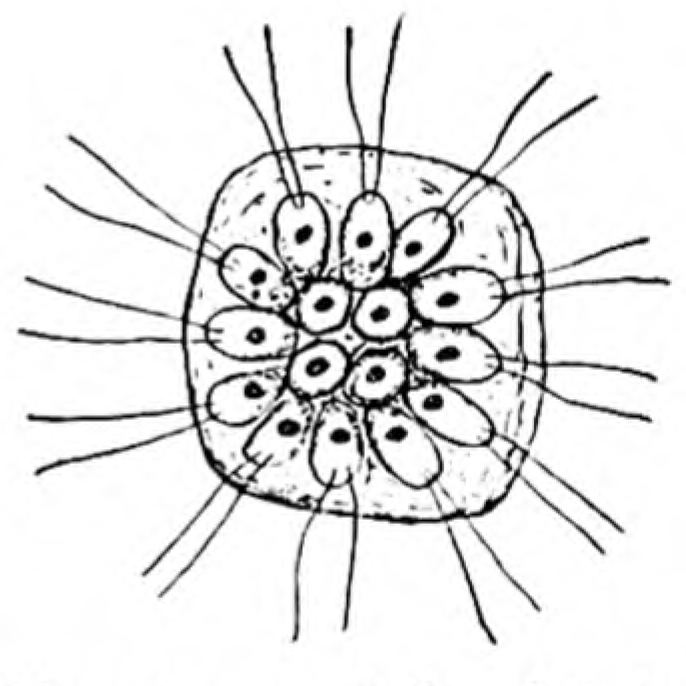
This genus is of peculiar interest to students of botany because the most characteristic swimming cells, both zoöspores and gametes, of green algae and of some of the fungi and higher plants are very much like individuals of *Chlamydomonas*. Such similarity of structure is usually considered to indicate a degree of relationship between the groups possessing it. It seems more than coincidence to find this type of cell in the life history of a large assemblage of diverse species. If these structures are the result of certain gene combinations, then the genes, in all probability, must have been derived from a common source, and the apparent relationships are based on actual descent from earlier ancestors.

REPRODUCTION. In the reproductive stages of *Chlamydomonas* the flagella disappear and the protoplast divides. If only one, two, or three divisions occur, making two, four, or eight new cells, they escape as zoöspores and have only to grow to full size to become mature. If, however, a larger number of divisions occurs making eight, 16 or 32 small, highly motile cells, they commonly act as gametes and fuse in pairs, lose their flagella, and form zygotes. The zygote later germinates, by a reduction division producing four haploid zoöspores which grow into adults. When three divisions take place, producing eight cells, they may act either as zoöspores or as gametes. What are the chromosome numbers in each step in this life history?

Sexual reproduction in *Chlamydomonas* illustrates a situation to be met at several points in succeeding studies. When, as in this case, the gametes are alike they are called *isogametes* (*isos*, equal). In the plant kingdom every gradation occurs between *isogamy* and extreme *heterogamy* (*heteros*, other), in which eggs and sperms are very different from each other.

GONIUM. The individual in this genus is a group of cells. *Gonium pectorale*, the species usually studied, is composed of 16 *Chlamydomonas*-like cells arranged in the form of a flat plate. Its reproduction is usually asexual. Each cell, by a series of 4 mitotic divisions produces 16 small



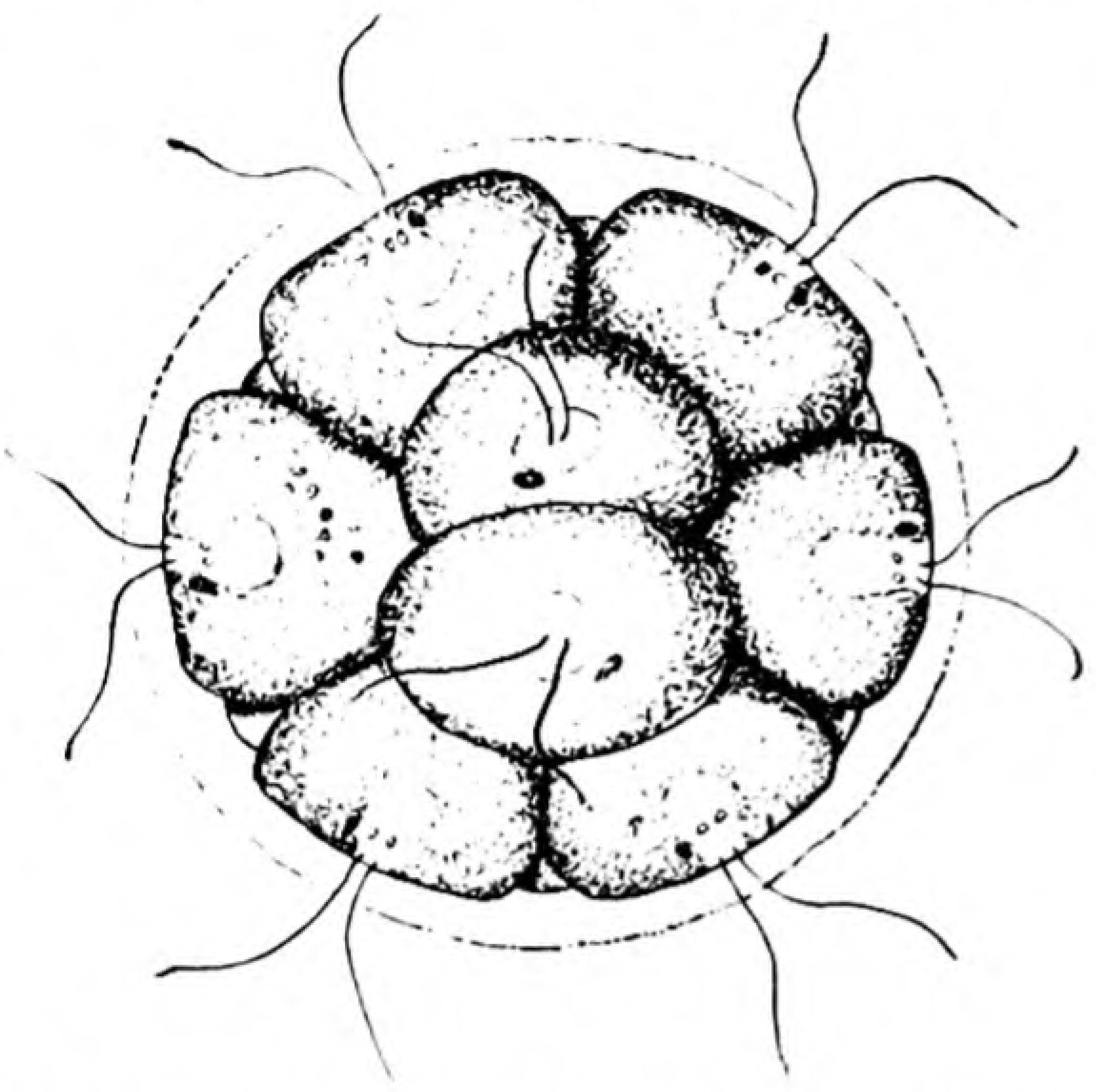


Above, *Chlamydomonas*. Left, adult individual; right, gametes beginning to fuse.
Below, *Gonium*. Flat colony of 16 *Chlamydomonas*-like cells, held together in gelatinous matrix.

cells which organize into a new small-size colony and escape. Isogamous sexual reproduction occurs when isogametes from different colonies unite and form a zygote. This germinates by a meiotic division, producing 4 haploid cells which became organized into a small colony.

PANDORINA. A colony of *Pandorina* consists of 16 or 32 cells resembling *Chlamydomonas* arranged in the form of a hollow sphere and held together in a gelatinous shell of pectin. The pair of flagella of each cell points outward and the concerted beating of all the flagella causes the colony to move about in the water.

REPRODUCTION. When this plant reproduces asexually each vegetative cell divides repeatedly, producing 16 cells which organize a new colony; or a similar division may result in the production of swimming gametes which fuse in pairs and form



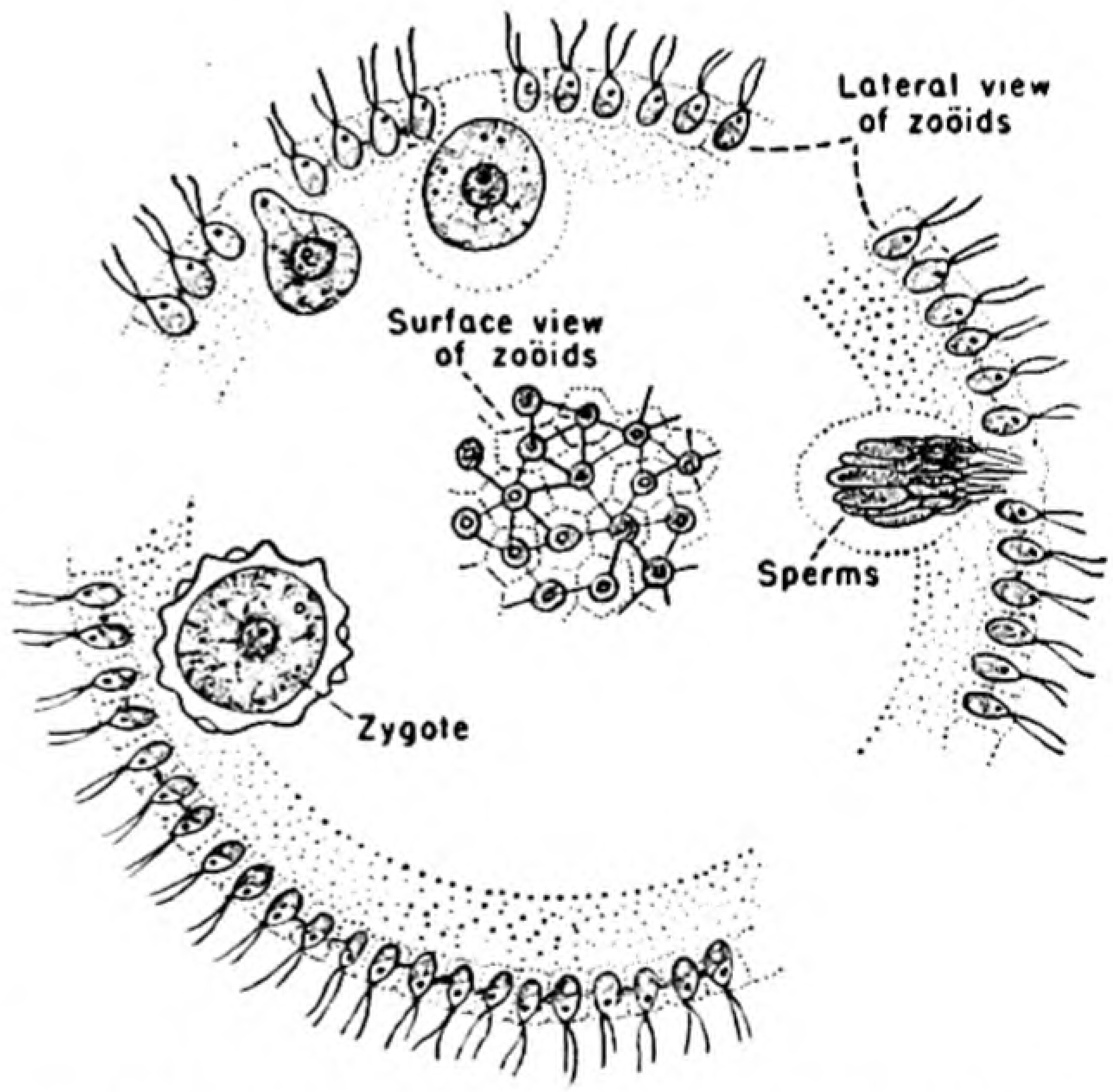
Pandorina spherical colony showing *Chlamydomonas*-like cells.

zygotes. The two fusing gametes are usually distinctly different in size, and this difference is regarded as evidence of a tendency toward heterogamy. When the zygote germinates it usually produces from one to four zoöspores, and each of these, in turn, divides into 16 zoöspores, which organize into a new colony.

VOLVOX. Long before good microscopes were available the attention of observers was attracted to the conspicuous rolling motion of the spherical green colonies of *Volvox*, large enough to be seen clearly with the naked eye. With the microscope, this organism proves to be a hollow ball whose surface is made up of thousands of small *Chlamydomonas*-like flagellated cells encased in a jellylike matrix. Structurally, *Volvox* is like a very elaborate *Pandorina* colony. These organisms move in one direction in such a decisive way, often toward the light, that there seems to be some sort of coördinating mechanism. Slender strands of cytoplasm which in some species can be seen extending through the gelatinous material from cell to cell, are possible channels through which impulses travel, permitting such unified action, though experimental proof of this theory is lacking.

REPRODUCTION. Old colonies of *Volvox* are frequently seen to have a number of small colonies inside. Each of these is formed from a single cell which begins to divide rapidly while still located in the gelatinous sheath. At first there is formed a small, saclike group of cells, which is much like an adult colony in structure and appearance. This sac now breaks loose from its attachment and becomes free inside the parent colony. After a time the old colony breaks down and the new ones escape into the water, thus completing the asexual type of reproduction.

In the steps preceding sexual reproduction certain cells enlarge greatly and develop into nonmotile eggs. Meanwhile, other cells of the same



Volvox. Sexual reproduction. (*Right*) Sperms forming. (*Above, left*) Eggs forming. (*Below*) Zygote with horney walls (all taken from sections of colonies). (*Center*) Surface view of colony showing protoplasmic connections between cells.

or other individuals divide, producing bundles of very small, active, terminally biflagellate sperms which soon separate and swim about. The union of a sperm and an egg initiates the formation of a thick-walled, spiny zygote, which later germinates

with a reduction division and produces a new small colony.

Euglenales. This order is of special interest because it contains both plantlike and animallike species. In all cases the individual is unicellular. In most of the genera each cell has a single long, whiplike flagellum, but in a few it has two, and in one genus it has three flagella.

In many species the cells have chloroplasts which produce much of their food, while in others that are obviously closely related to them, chlorophyll is entirely lacking. These almost colorless organisms absorb their food from outside sources in an animal-like or funguslike manner. A single representative of this peculiar order will be discussed here.

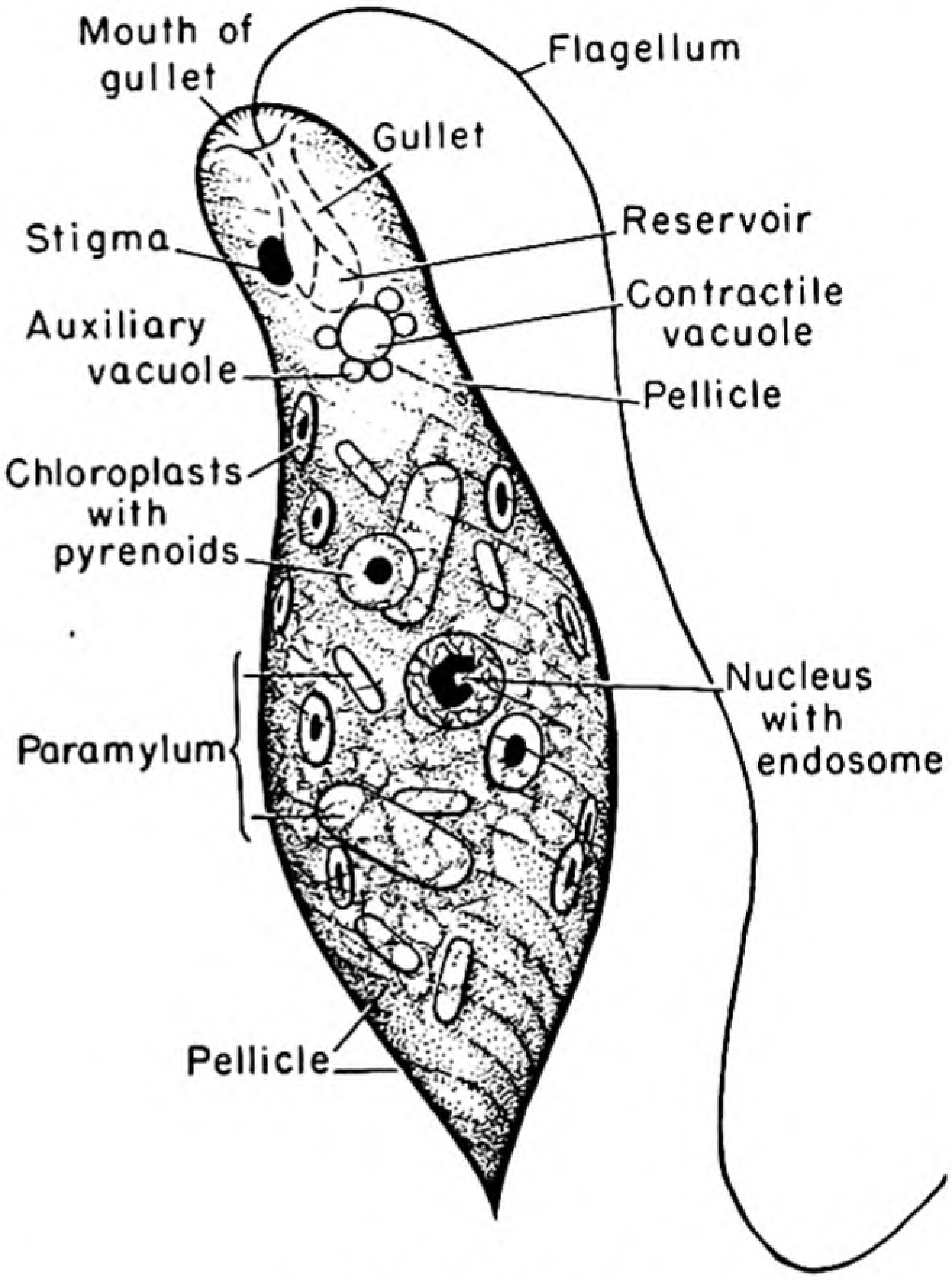
EUGLENA. The various species of *Euglena* are especially likely to thrive in stagnant water that is heavily loaded with decaying organic matter. In hog wallows, water holes for cattle, and slow-flowing, badly polluted rivers these organisms sometimes become so numerous that they color the water green, or even form over the surface green layers with the consistency of cream.

When examined with the microscope the individual of *Euglena viridis*, one of the species most often studied in the laboratory, is found sometimes to swim freely by means of a long whiplike flagellum attached in front, and sometimes to creep animallike across the field of view. When swimming, the cells elongate until they assume a broad spindle shape rounded at the front end.

The organism does not have a true cell wall; instead, the surface of the protoplasm is both firm enough to maintain its shape and sufficiently elastic to allow the cell to squirm about in a wormlike manner or to round up into a ball.

Within the protoplasm there are several elongated oval chloroplasts with the usual chlorophyll-carotinoid pigments. *Euglena viridis* is capable, therefore, of carrying on photosynthesis. The reserve carbohydrates take the form of a peculiar starch called *paramylum*.

At the front or anterior end of the cell several important features are centered. One of these is a funnellike opening through which the flagellum extends outward from the cytoplasm. At the base of the funnel is a circular *reservoir* into which a *contractile vacuole* empties. This vacuole is a space within the cytoplasm which gradually fills with liquid and then discharges its contents into the reservoir, and thence into the water outside the cell. This action is repeated several times a minute.



Euglena sciotensis.

Contractile vacuoles are very common in primitive animals (Protozoa). Likewise, they occur in all the Volvocales, in Euglena and its nearest relatives, in some of the Chrysophyta, and in reproductive cells of several others. They are variously interpreted as having the function of excretion and of reducing excess water in the protoplasm.

Near the reservoir there is a reddish stigma which is thought to be a carotinoid much like that of the visual pigments in the retina of the eyes of higher animals, and it is usually interpreted as being sensitive to light.

Sexual reproduction is unknown in *Euglena*, increase in numbers resulting from mitotic divisions.

Euglena is of the greatest interest to the botanist because it has plant and animal characteristics so

evenly balanced that it is described in both botanic and zoologic literature. The most distinctive plant structure is the chloroplast, while the absence of a cellulose wall and the ability of some *Euglenas* to absorb organic food from outside sources are both definitely animallike. In addition, some of the undoubted relatives of Euglena are distinctly green algae, while some others have no chlorophyll and are clearly primitive animals. For a variety of reasons it has been suggested that the family of organisms to which Euglena belongs may have developed from forms that were more or less intermediate between the green and golden algae, and that out of this assemblage has arisen the animal kingdom. It seems, then, that *Euglena* is on the "continental divide," with plants extending away in one direction and animals in the other.

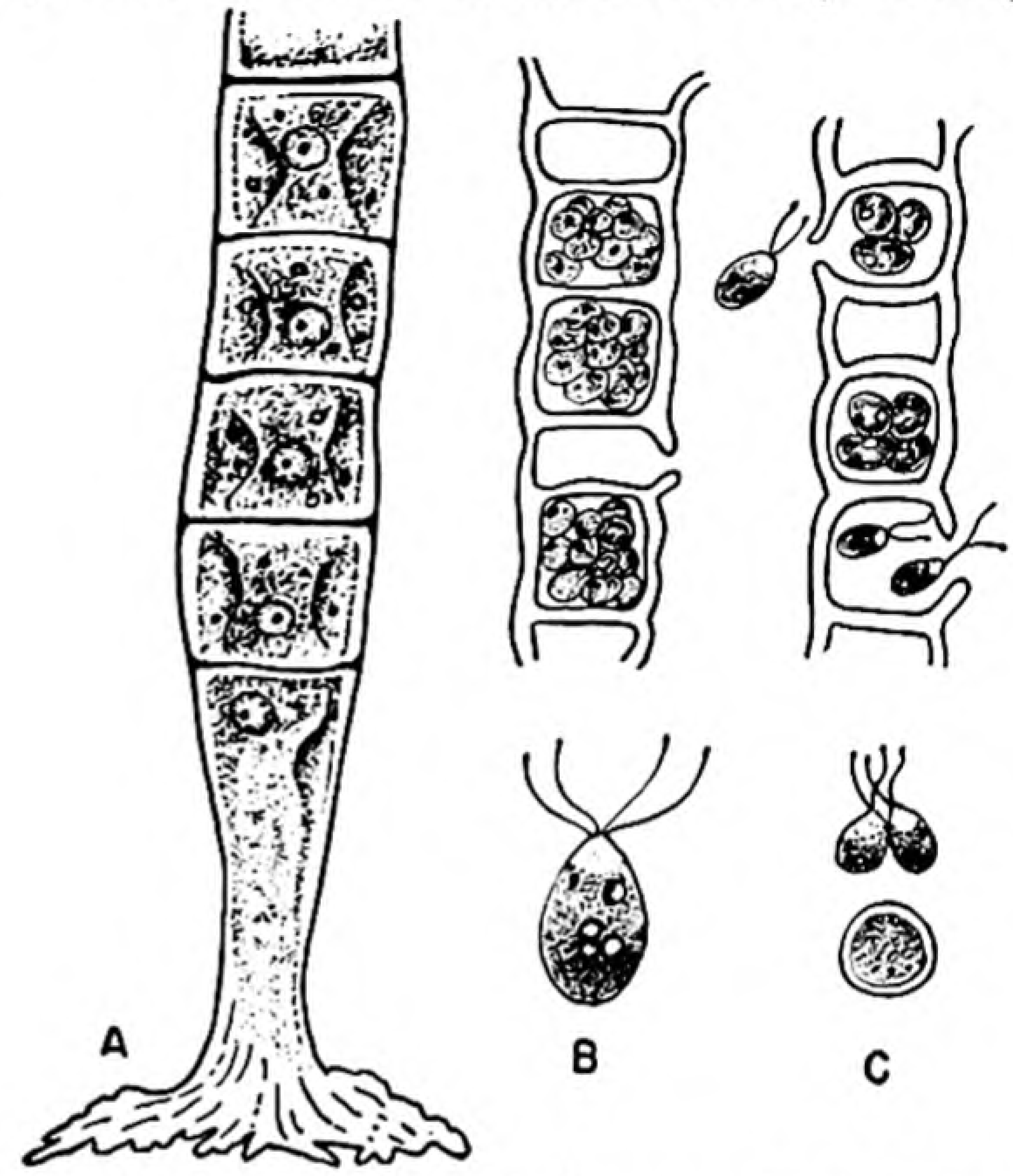
Ulotrichales. This is an order characterized by terminally biflagellate or sometimes quadriflagellate reproductive cells, of the *Chlamydomonas* type. The plant body takes the forms of unbranched or branched filaments, thin plates of radiating cells or, in one case, of an irregular colony of almost independent cells.

ULOTHRIX. The various species belonging to this genus are to be found free-floating or attached to such solid objects as sticks, rocks, etc., in streams, water troughs, and sometimes quiet pools. Almost all live in fresh water and are most abundant in spring and fall, when the water is cold.

REPRODUCTION. This alga grows as slender, unbranched filaments. Asexual reproduction takes place by the production of numerous zoöspores which resemble *Chlamydomonas* except that they have four terminal flagella instead of two. These zoöspores swim about for a time and then attach themselves to some support before developing into new filaments. Sexual reproduction involves the fusing of biflagellate isogametes, from different plants. The zygotes undergo meiosis, forming four zoöspores from each zygote. This genus is very important in interpreting the relationships of the higher plant groups and therefore it is especially important to keep the details of its structure and simple life history in mind.

COLEOCHAETE. The body of this plant assumes a somewhat circular flat form. Numerous individuals may often be found clinging to the leaves of plants in fresh water, especially water lilies and cattails.

The plant body is usually only one cell thick. It may be compact and disklike or it may be deeply

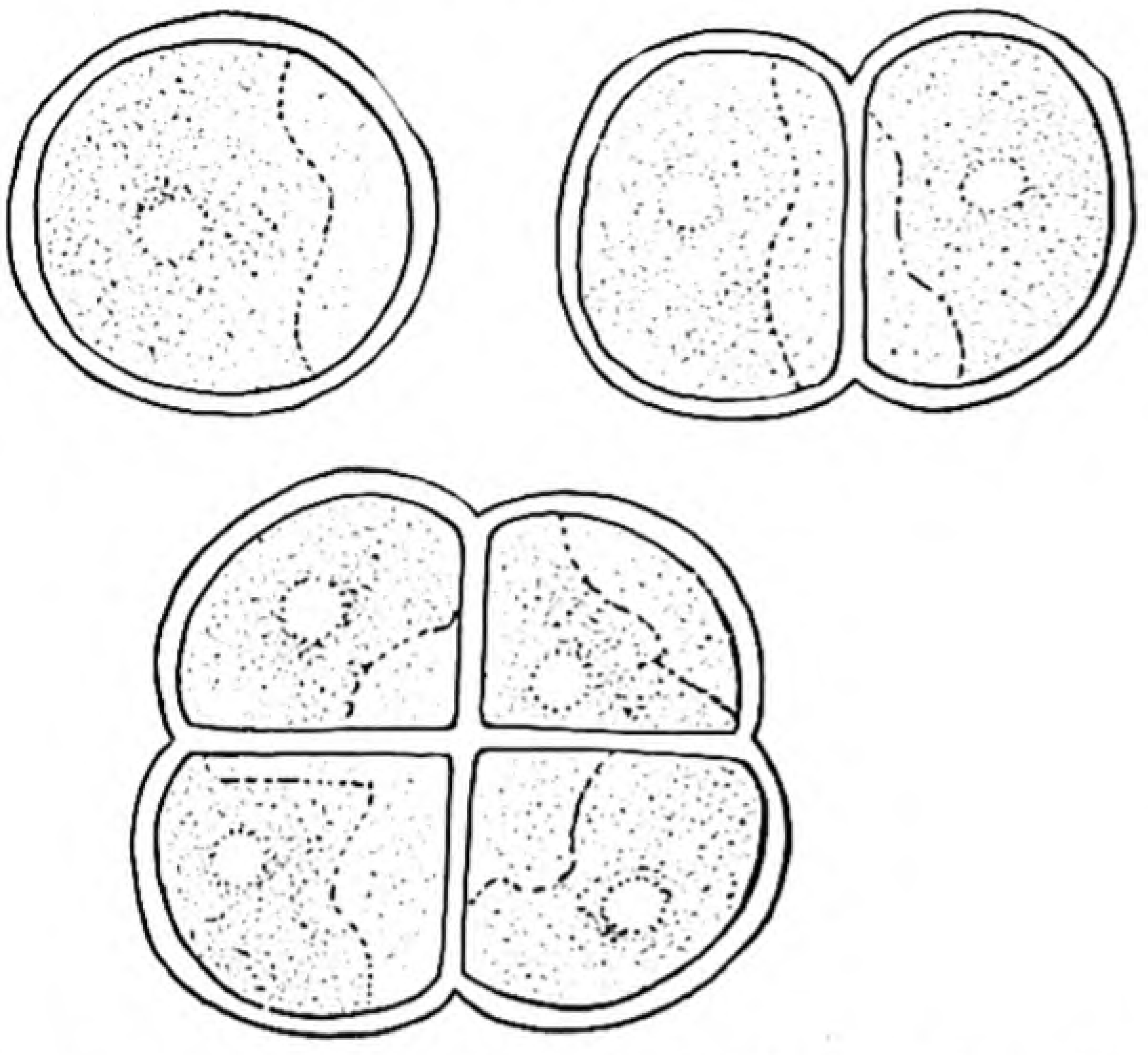


Ulothrix. (A) Base of filament with holdfast and with characteristic ring-shaped chloroplasts in vegetative cells. (B, *top*) Cells containing gametes. (C, *top*) Cells containing two and four zoöspores. (B) Zoöspore, greatly magnified. (C) Uniting gametes and a zygote. (B, *top* and C, *top*) after Tilden, after West.

lobed and is often more than an eighth of an inch in diameter.

REPRODUCTION. Zoöspores, which are terminally biflagellate, are produced much as in other algae. The chief interest in the genus is centered in its method of sexual reproduction. The motile sperms are produced singly or in small numbers in an *antheridium.* The oögonium has a long beaklike projection, through which the sperm enters in reaching the nonmotile egg. After fertilization, the vegetative cells of the thallus grow over the zygote, covering it with a layer of tissue. At the end of a period of dormancy the zygote divides with a reduction division. Mitotic divisions follow, producing a rather extensive haploid structure each cell of which later forms a zoospore and finally a new plant. Here, again, the zygote constitutes the entire sporophyte generation.

PROTOCOCCUS. This alga is frequently known also as *Pleurococcus*. It is to be found in the more humid climates of the United States on old, unpainted buildings and fences, on damp stone walls,



Protococcus, showing individual cell, and simple colony formation. Note nucleus and irregular chloroplast in each cell.

and especially on the shaded sides of tree trunks. It makes up the greater part of the "moss" which woodsmen and members of scouting organizations use to guide them through the forests. Because it grows more luxuriantly on the north sides of trees than on the others, it may serve as a crude compass by which persons can find their way about in the woods.

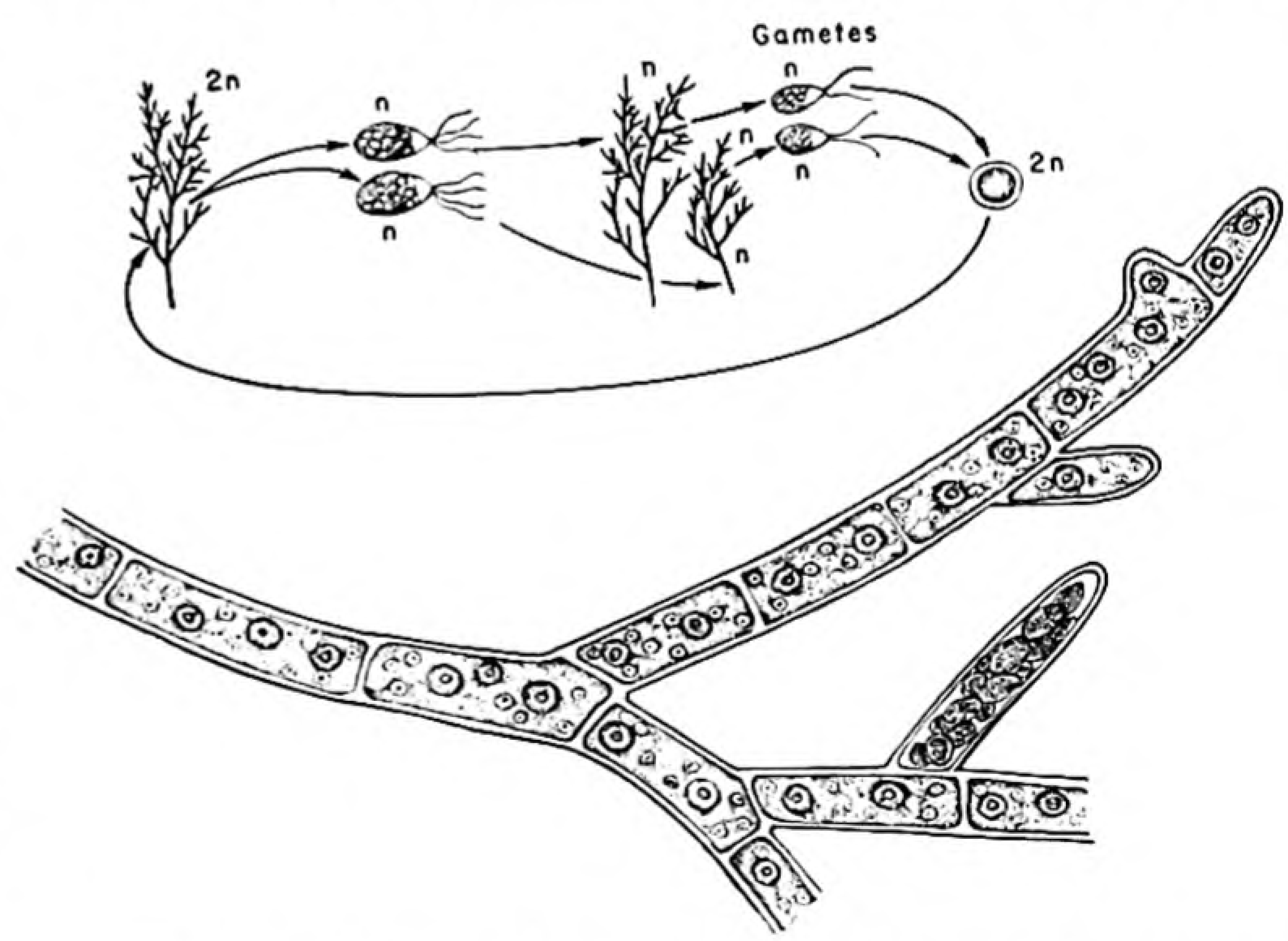
A good growth of the alga resembles a thin coat of green paint. The microscope shows it to consist of single separate cells or of small colonies of various shapes. The cell has a nucleus and one, or possibly more than one, irregularly lobed chloroplast. Ordinary cell division is the only kind of reproduction known. It is, therefore, impossible to be certain which groups of green algae are its nearest relatives.

This alga may remain dry for months, only to resume growth activities with the return of moisture. In this respect *Protococcus* behaves much like many of the plants of deserts that are able to endure great loss of water without permanent damage.

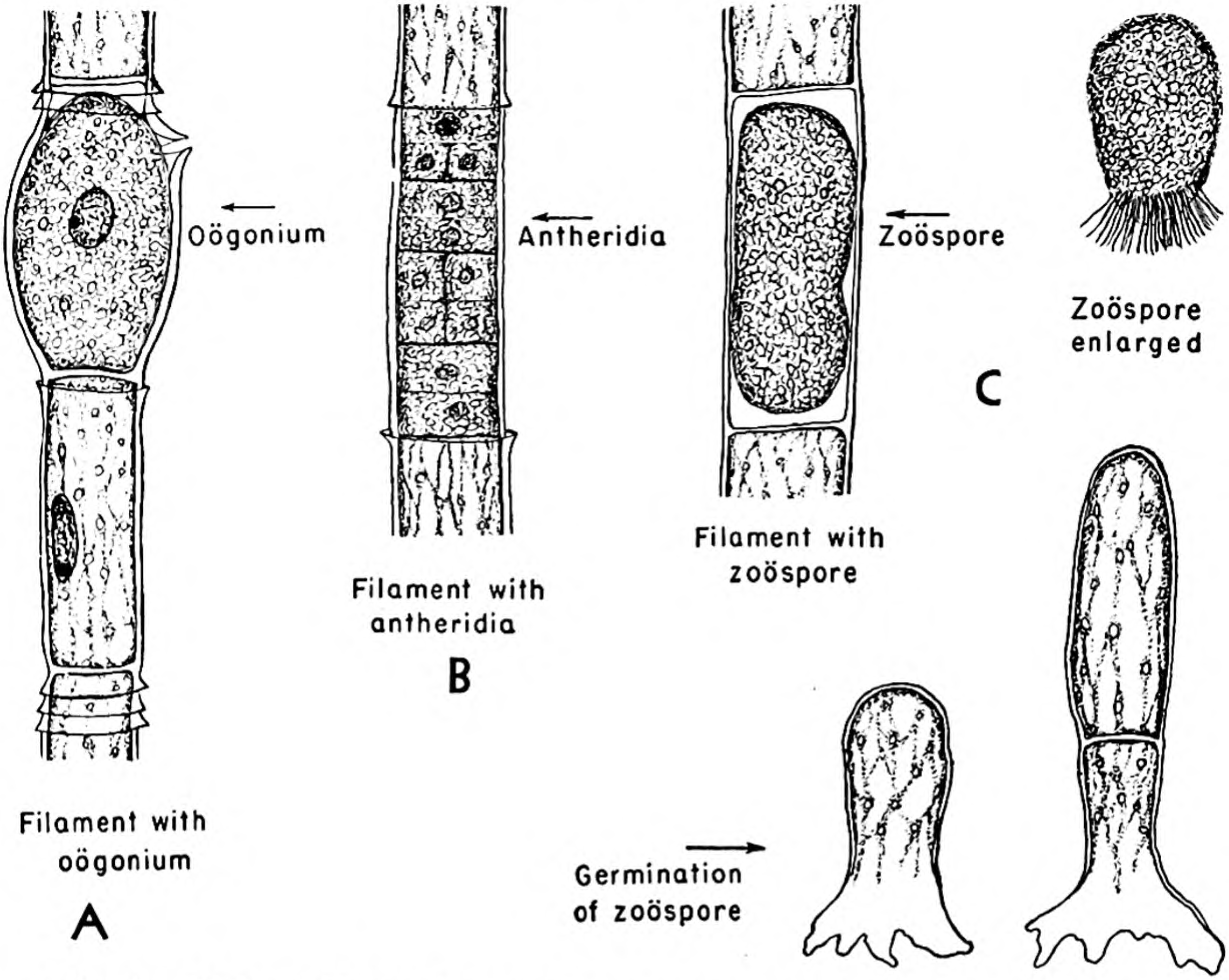
CLADOPHORA. Plants of this genus contrast with those described above mainly in that each cell of *Cladophora* contains many small nuclei. Multinucleate organisms are known as coenocytes. They develop when a great many nuclear divisions occur, but walls do not form. This plant with its occasional cross walls is called a *partial coenocyte*.

Cladophora is one of the commonest of all green algae. It grows attached to objects both in fresh water and in the sea. The filaments are so firmly constructed that they can withstand a great deal of violence by flowing water or wave action. This plant often attaches itself to turtles, alligators, fresh-water mussels, and other moving objects, thus traveling through the water. The filaments are much branched and frequently grow to a length of several inches. Each cell contains numerous round or angular chloroplasts. Close examination frequently shows these to be arranged in irregular rows corresponding to plates of more dense cytoplasm, which tend to separate the cell contents into a number of parts.

REPRODUCTION. *Cladophora* of certain marine species exhibits a definite alternation of sporophyte and gametophyte generations which have the same



Cladophora. (*Top*) Life history of a marine species. (*Bottom*) Portion of a fresh water plant showing the numerous nuclei (small, circular bodies) in each protoplast. One branch contains numerous gametes.



Oedogonium. (A) Plant with oögonium, containing egg. At upper end of oögonium may be seen the pore through which the sperm enters; also, ringlike "caps." (B) Filament with eight antheridia in which sperms are forming. (C) Zoöspores; (*top, left*) one is forming from vegetative cell; (*bottom*) two stages in development of holdfast and filament.

appearance. The diploid or sporophyte plants produce numbers of zoöspores, each with four flagella. A reduction division takes place when they are formed, resulting in haploid spores. They swim about for a time and finally attach themselves to some solid body and grow into new gametophyte plants.

The gametophytes organize numerous biflagellate isogametes. These fuse in pairs, forming zygotes which in due time develop into new sporophyte plants capable of producing zoöspores, thus completing the life cycle.

In fresh-water species of *Cladophora* the conspicuous plant is a gametophyte. Reduction division occurs when the zygote germinates. The zygote, therefore, is the only cell of the sporophyte generation.

CHAETOPHORA grows in the form of small, shining, green beadlike masses attached to sticks and leaves in the water. Each mass consists of a system of radiating, branched filaments imbedded in a firm gelatinous matrix. The plant takes its name from a long, bristlelike appendage (*chaete*, a bristle) which is borne at the end of each filament. The life history is almost identical with that of *Ulothrix*.

Oedogoniales. This order contains three genera, but only one of them, *Oedogonium*, is commonly studied. The following description of that genus satisfactorily distinguishes the entire order.

OEDOGONIUM. *Oedogonium* has received a great deal of attention from botanists because it is peculiar in several respects. The plant body is an unbranched filament, sometimes as much as a few inches long. The various species occur in free-floating, tangled masses or attached to sticks, grass blades, petioles of water lilies, or leaves of cattails in streams and ponds. The attached forms are anchored by means of a specialized cell at the base of the filament which acts as a holdfast. Under the microscope the genus can be distinguished by the fact that one end of each cell is of larger diameter than that of the other, and by caplike markings at the upper ends of some of the cells, resulting from a peculiar method of wall formation.

The cell wall is thick and tough. The chlorophyll is located in what may be regarded as one chloroplast cut into a number of shreds or as a compound structure composed of many long chloroplasts loosely attached to one another, forming a plate curved around inside the wall. Each cell has a single nucleus.

Oedogonium is one of the very few exceptions to the general rule that the swimming cells of green algae are terminally biflagellate or quadriflagellate. In this genus both the zoöspores and the sperms have a crown made up of large numbers of flagella.

REPRODUCTION. The zoöspores, by means of which the plant reproduces asexually, are among the largest uninucleate ones known in the algae. Only one is produced in a cell. One end of the spore is colorless and is surrounded by a circle of flagella. This colorless spot, together with the flagella, forms the holdfast when it attaches itself.

Sexual reproduction is always heterogamous, but it varies somewhat in the different species. Two general types may be recognized and will be described here. In one of these, a few cells in the filament enlarge and the contents of each shrinks slightly and becomes an egg. The cell wall inside which an egg organizes is known as the *oögonium*. Certain other short cells, formed by a series of rapid divisions, change into *antheridia*, each of which produces two sperms. Each sperm is provided with a crown of many flagella with which it can swim freely. A sperm, entering the oögonium by a specialized opening, fuses with the egg, making a thick-walled zygote which is, in reality, a sporophyte. The zygote germinates by meiotic divisions, producing a tetrad of four zoöspores, each of which attaches itself and grows into a new plant.

In some other species of *Oedogonium* the oögonia develop in the same way as those just described, but the antheridia are produced on peculiar dwarf male plants only two or three cells in length. These male plants grow from small zoöspores known as *androspores* and are produced in specialized small cells of the filament.

Zygnematales. This is the only order of the green algae, with one possible rare exception, in which there are no cells of any kind with flagella. The method of sexual reproduction, to be described below, is also entirely distinctive.

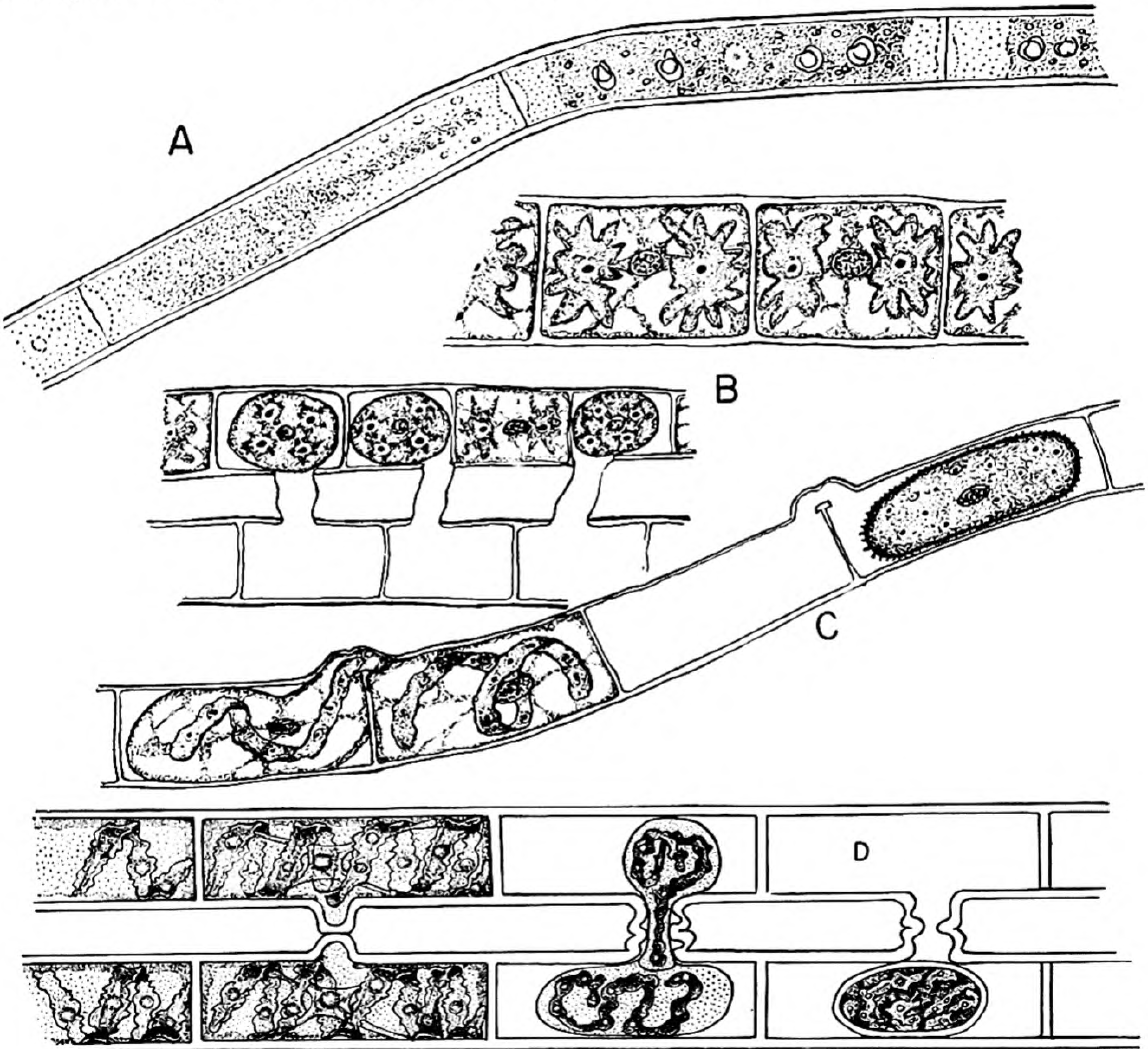
SPIROGYRA, ZYGNEMA, AND MOUGEOTIA. Among the most conspicuous of the green algae are a number of genera whose filaments form large floating masses in ponds or lakes and in quiet places in streams. These masses of tangled threads frequently remain at the surface in clear, warm weather and sink in cool, cloudy weather and at night. This behavior may be due partly to changes in temperature, but the main factor causing it is the bubbles of oxygen released by photosynthesis. The frothy appearance caused by the bubbles entangled among the filaments on clear days is partly responsible for the prevalent idea that these plants are unclean.

A microscopic examination usually shows that, although small numbers of other plants are present, these floating scums are most often made up largely of three genera, *Spirogyra*, *Mougeotia*, and *Zygnema*.

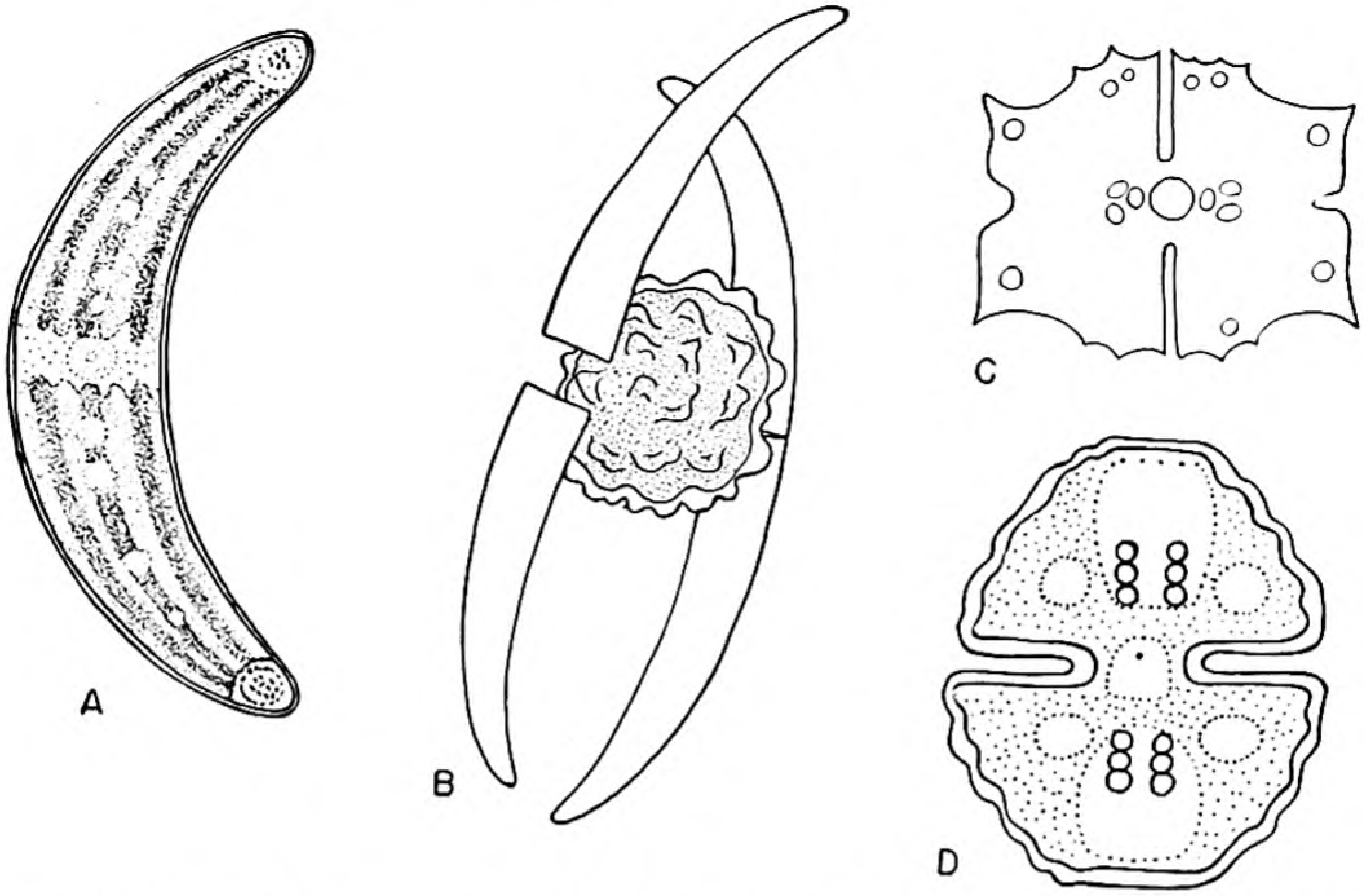
All of these grow in the form of long, silky, unbranched filaments, each made up of a single row of cylindrical cells. The common name, water silk, is often applied especially to *Spirogyra*, although it is equally suitable to all three genera. The filaments are covered with a thin layer of gelatinous pectic material which gives them a smooth, slippery consistency. By continually sloughing off on the outside as it is produced from within, it keeps the filaments clean. These plants can usually be recognized in the field by a combination of three characteristics: they are the clear, bright, grass-

green color, definitely contrasting with blue-green algae; a soft, smooth, silken feel when rubbed between thumb and fingers; and a peculiar coiling of the slender threads into a long spiral at the lower end when a mass is lifted out of the water.

The most noticeable feature of the cells is the chloroplast. In *Mougeotia* this is a flat plate as long as the cell, and usually twisted once. In *Zygnema*, which always has two in each cell, it is star-shaped. *Spirogyra* has from one to four or more spiral bands in each cell, the number being somewhat characteristic of the different species. Each chloroplast has from one to several specialized structures, the *pyrenoids*. These are small bodies of



Spirogyra, *Zygnema*, and *Mougeotia*. (A) Two cells of *Mougeotia* showing the flat, slightly twisted chloroplasts with dark colored pyrenoids scattered through them. In the cell to the left the chloroplast is seen in edge-wise view. (B) *Zygnema*. (*Top*) Showing star-shaped chloroplasts; (*bottom*) two filaments in which conjugation is complete, with a row of zygotes in the upper filament. The second cell from the right has failed to conjugate. (C) *Spirogyra* belonging to a species in which adjacent cells of the same filament fuse, producing zygotes. (D) The more usual type of *Spirogyra* in which conjugation takes place between cells of neighboring filaments, showing steps in the process.



Desmids. (A) *Closterium*, showing the nucleus in the middle and a series of pyrenoids extending to the ends of the striate chloroplasts. At the ends of the cell are small pockets of gypsum crystals. (B) A zygote of *Closterium* with the empty cell walls of the individuals that have just conjugated. (C) *Euastrum*. (D) *Cosmarium*. (Conjugation, after Wolle; the other specimens redrawn from Smith: "Phytoplankton of the Inland Lakes of Wisconsin.")

protein around which grains of reserve starch accumulate. They are sometimes considered to be peculiar organs of food storage.

The cell has a single nucleus, but this cannot ordinarily be seen very satisfactorily except in specially prepared and stained material. The filaments grow in length by transverse division of the cells, the actual separation of the protoplasm being preceded by the mitotic division of the nucleus much as in higher plants. As the cell divides, the chloroplasts are pinched in two, maintaining the characteristic number.

REPRODUCTION. Sexual reproduction in *Spirogyra* usually occurs in spring and summer. When conditions are right, any two cells that chance to come in contact with one another are likely to act as a pair of gametes. At the point where the walls of these cells touch, tubelike extensions develop, forming a passageway between them. The protoplasm of each loses a considerable amount of water by means of contractile vacuoles and therefore reduces in size. One of these protoplasts now slips through the passageway, called the *conjugation tube*, and unites with the other, forming a thick-walled zygote. With the disintegration of the filament the zygotes fall away into the mud, where they remain until the return of conditions suitable for growth.

The various species of *Spirogyra* exhibit only slight deviations from isogamy. In some, the zygotes form equally readily in the cells of both plants of a conjugating pair; in others they organize in the middle of the conjugation tube, and in a few instances adjacent cells of the same filament unite. On the other hand, in a few species all the zygotes form in the cells of one of the plants, which is regarded as the female.

Zygnema and *Mougeotia* carry on conjugation in a manner that is almost identical with that of *Spirogyra*.

On the return of conditions favoring growth the zygotes germinate, giving rise to young filaments similar to the parent plants. The zygote is a diploid cell and reduction division occurs as the first step in germination. The vegetative plants are all haploid, that is, they are the gametophytes. Once again, the zygote is the only sporophyte cell.

Although the adult filaments are usually not attached to anything, the young plants developing from zygotes frequently have a definite *holdfast* cell by which they may for a time remain attached to objects. Later, however, all of them break loose and float freely in the water.

DESMIDS. In examining collections of algae to select specimens for study, the student frequently encounters certain unicellular or colonial forms which are so conspicuous that they command immediate attention. Among these are the desmids and diatoms. The latter have been discussed as representatives of Chrysophyta. The two groups are not at all closely related, but frequently are found growing together in fresh water.

The members of the family, Desmidiaceae, are frequently referred to by the English name, desmids. They are of a brilliant green color when alive. Each individual is a single cell that is of beautiful form and often highly ornate. The forms assumed are numerous, ranging from intricate star-shaped patterns to simple, plain crescents like those of the new moon. Sometimes a number of individuals cling together, forming filaments, but they are to be regarded as essentially unicellular.

Although the cell assumes many bizarre shapes in the different genera, it is, when fully grown, always symmetrical; that is, it consists of two parts which are exactly alike and often are connected by a noticeably constricted portion, the *isthmus*.

The cell contains two fluted or lobed chloroplasts, one in each half. The nucleus is usually located at its center or in the isthmus. In some species there is, in each end, a conspicuous vacuole containing a number of small crystals of gypsum which are in constant motion. This is not a life movement but is due solely to physical causes. It is known as "Brownian movement" because of its having first been reported by the British botanist, Robert Brown, more than a century ago.

REPRODUCTION. Since a desmid is unicellular, new individuals form by mitotic division. The new cells are asymmetric in outline, but within a few hours each grows a new part, causing it to resemble the parent. The single chloroplast contained in the young plant soon divides, and one part goes into the newly-formed portion. This asexual method is the most frequent means of increasing the numbers of individuals.

There is also a sexual method of reproduction. Two cells come near together and are connected by a conjugation tube in which the contents meet and fuse much as in some species of *Spirogyra*. The zygote forms a thick wall which is usually ornamented with warts or spines.

The behavior of the nucleus during the formation and germination of the zygote is obviously difficult to observe. It is practically certain, however, that the nuclei of the two gametes unite, and that the resulting nucleus undergoes a reduction division as the zygote germinates. Another division results in the characteristic four nuclei, but one, two, or three of these may disintegrate. The remaining one or more become the nuclei of new individuals.

If two desmids go into the formation of the zygote and only one or two appear when it germinates, the significance of the process may be questioned. One part of the answer is that zygotes usually remain dormant until the next growing season, thus carrying the species over periods of winter or drought. It is also thought that here, as in other plants and animals, the combining of two cells into one, and the separation of this to form new ones, results in a beneficial interchange and reassortment of genes.

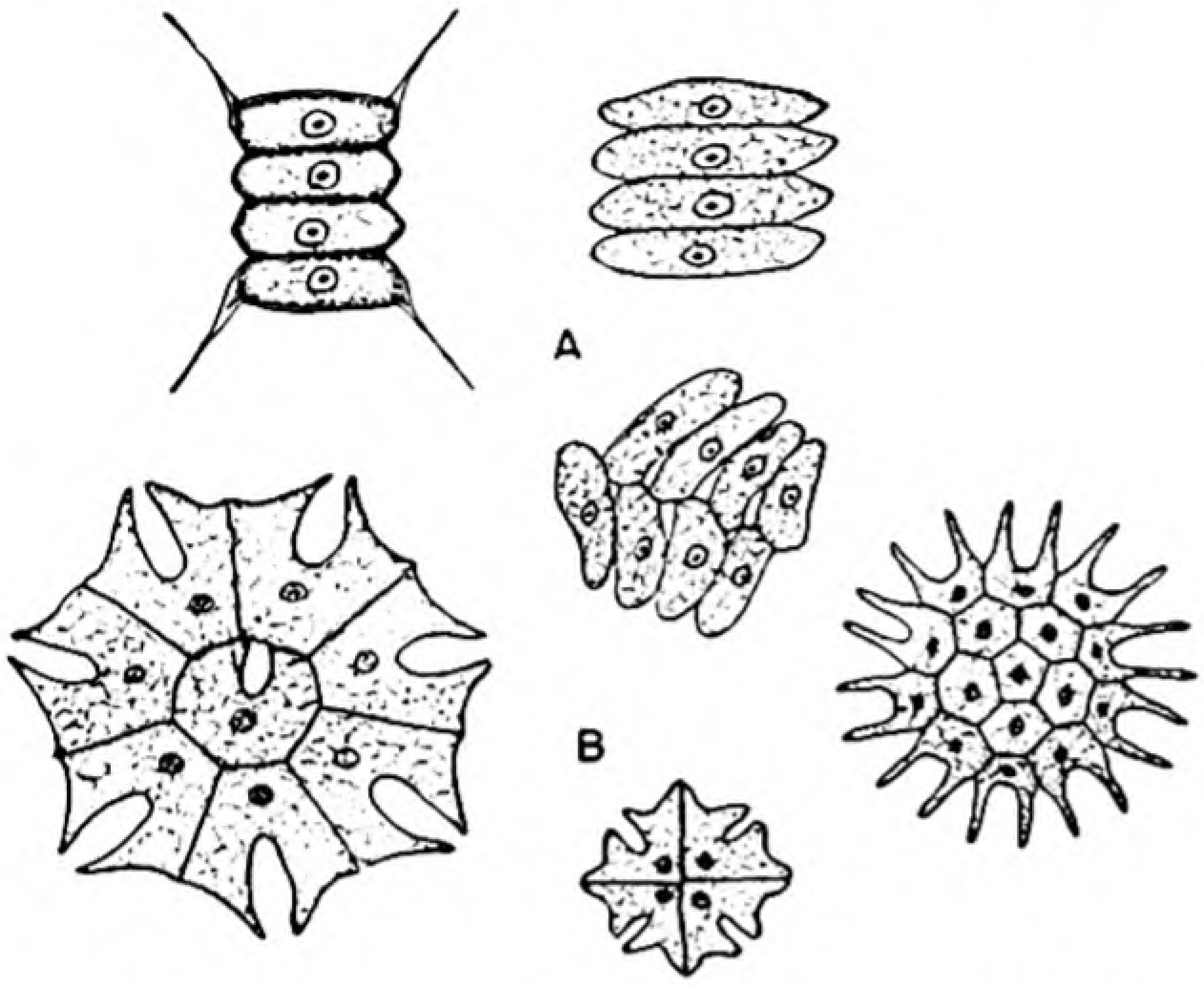
In the life history it is evident that the actively growing desmid represents the gametophyte generation, and the zygote corresponds to the sporophyte.

Chlorococcales. In this order neither mitosis nor meiosis occurs except in connection with the reproductive processes. In other words, there is no increase in cell numbers after the colonies are organized.

PEDIASTRUM AND SCENEDESMUS. These small floating algae occur in the form of microscopic flat platelike colonies, each consisting of some number of cells which is a multiple of two. Colonies of *Scenedesmus* usually have two, four, or eight cells, while eight, 16, and 32 are the numbers most often found in *Pediastrum*.

REPRODUCTION. In *Pediastrum* asexual reproduction takes place when any cell divides repeatedly,

producing as many biflagellate zoöspores as there are to be cells in the new colony. These escape, surrounded by a delicate retaining membrane, within which they quickly drop their flagella and become attached to each other in the usual *Pediastrum* pattern. Growth in size brings about the ornate, symmetrical form characteristic of the species.



Scenedesmus and *Pediastrum*. (A) Three colonies of *Scenedesmus*, one of which has hornlike extensions from the two end cells. (B) Three characteristic colonies of *Pediastrum*.

Pediastrum also reproduces sexually. Biflagellate isogametes unite, forming the zygote which continues to enlarge for some time. Zoöspores are formed by a series of divisions. These escape and swim about independently before coming to rest. After a time each one produces a packet of zoöspores confined in a membrane. Then follows the organization of a new colony.

Scenedesmus has no flagella but colony formation takes place within the parental cell wall as it does in *Pediastrum*. Sexual reproduction is unknown in this genus.

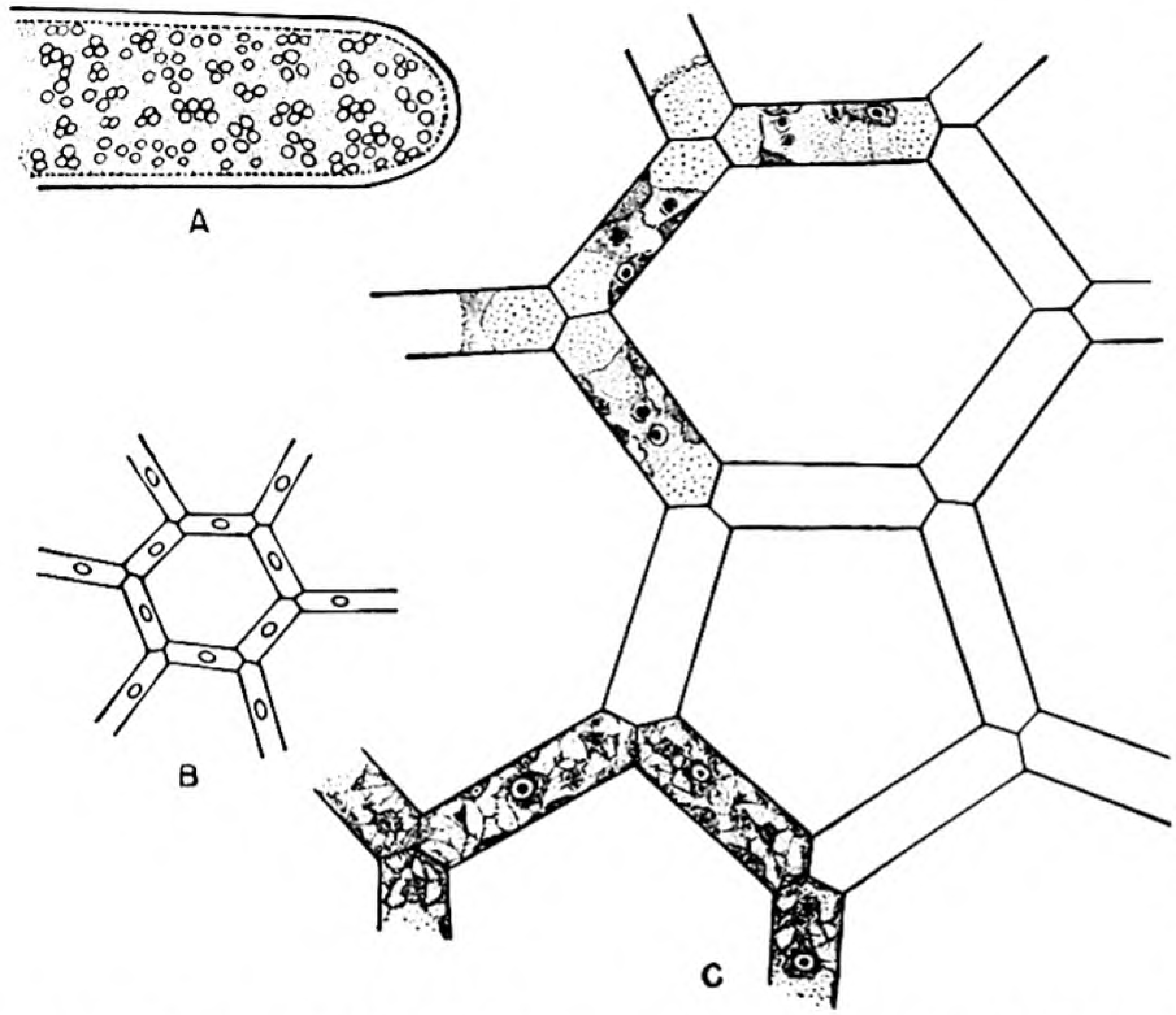
HYDRODICTYON. This plant, commonly known as waternet, grows in many ponds and streams over the earth. It is most luxuriant during the latter part of summer when it sometimes almost fills ponds and pools. The plant body consists of thousands of long, cylindrical cells joined together in such a way that they form the five- and six-sided meshes of a saclike net closed at both ends and often more than a foot long. As usual in this order there is no increase in number of cells except at the time when the colony organizes. The nets enlarge only by the growth of the individual cells. Young nets may form perfectly but, as they become older, they are torn and damaged so that only fragments remain, but the parts which have escaped injury are apparently as healthy as if their neighbors had not been destroyed.

The mature cells are cylindrical. Most of their cytoplasm forms a lining inside the wall, while the center is occupied by a gigantic vacuole filled with liquid. Each of the small cells of the young nets has a single nucleus, but the nuclei multiply by mitotic division. Wall formation does not take place and therefore the fully grown cell, which may be half an inch long, has thousands of nuclei distributed within the cytoplasm, forming a large coenocyte (*koinos*, pertaining to the community; *kytos*, vessel or cell).

REPRODUCTION. Old, fully developed plants may produce new colonies asexually by a series of very peculiar steps. The process can often be started by bringing old nets into a warm room late in autumn. At this time the number of nuclei in each cell is very large, some estimates indicating that there may be as many as 10,000 to 30,000. Around each nucleus and its bit of cytoplasm there now forms a membrane. Each one of these minute cells develops two terminal flagella and becomes a *Chlamydomonas*-like zoöspore. These swim around for a time inside the old wall and then elongate slightly, arrange themselves in such a way as to form a new net, become attached to each other and drop their flagella. The wall of the old cell soon disorganizes and the young net is set free.

Hydrodictyon also reproduces sexually. The adult cell divides much as in asexual reproduction but the motile structures produced are more numerous, probably as many as 100,000 forming in some instances. These escape into the water and soon many of them unite in pairs, forming zygotes. The zygote develops the usual heavy wall and may remain dormant for a time. When it germinates it produces a small number of zoöspores each of which enlarges and takes on an irregular form, finally organizing 200 to 300 other zoöspores.

These form a small net in the usual way. When the cells of this net grow to maturity each is able to develop a new net of ordinary size.



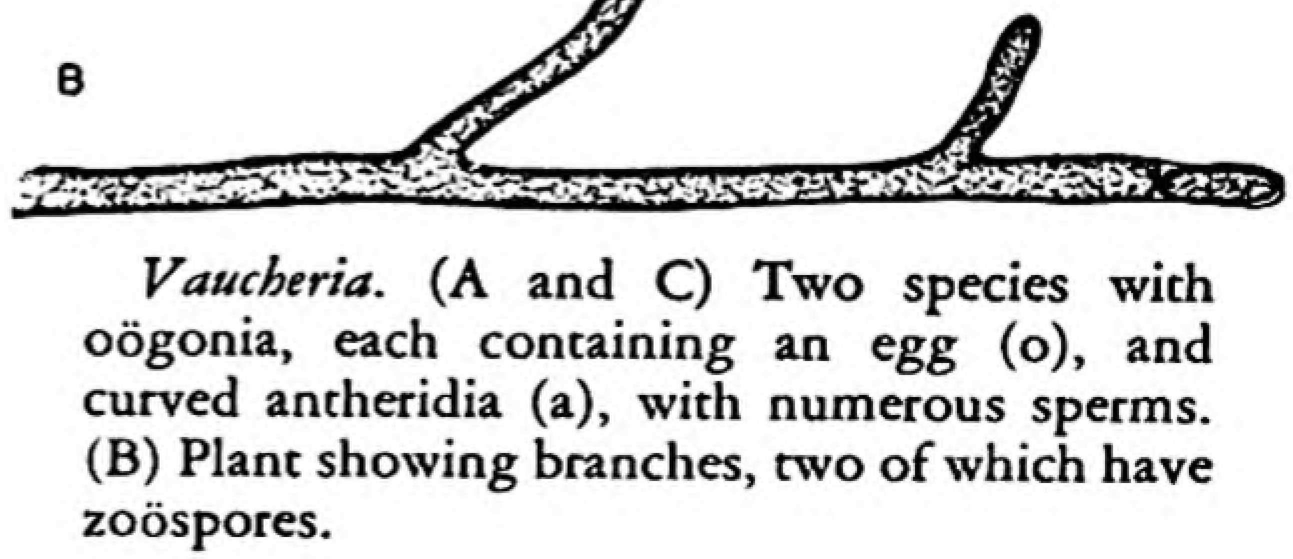
Hydrodictyon. (A) Old cell with new net beginning to organize inside its walls. (B) A few cells of young net. Note that they are uninucleate. (C) Older net made up of coenocytes

Without knowing more of the chromosome history it is difficult to correlate this life cycle with the typical one showing alternation of generations. It seems likely, however, that reduction division comes at the time at which the zygote produces zoöspores. If this is the case, the greater part of the life cycle is spent in the form of the gametophyte generation.

Siphonales. The plants belonging to this order are largely marine, but the one genus, *Vaucheria*, is chiefly freshwater and terrestrial. The order is remarkable because the vegetative plant is a complete coenocyte. The plant body is usually a branched tube lined with a firm layer of cytoplasm in which are embedded numerous small nuclei and disk-shaped chloroplasts. Occupying the center of the tube, inside the peripheral cytoplasm is a large, continuous, sap-filled vacuole.

VAUCHERIA. The different species of *Vaucheria* assume several distinct forms. Some species need to be continually wet with moving well-aerated water. These grow in thick, flat, felt-like pads, sometimes six inches or more in diameter, attached to rocks in shallow running water or exposed to the spray around waterfalls. Others float like *Spirogyra* in still water. As a rule, these two types are very sensitive to changed conditions and decompose so quickly after being taken out of the water that they should be examined almost immediately. They are usually at their best early in the spring, or even in winter, while the water is cold. Another kind is very common in late summer or autumn on wet ground around bodies of water or even in greenhouses or in moist, shaded places on cultivated soil. The terrestrial form is much less easily damaged and more suitable for study than the aquatic species.

The plant body is a rough, irregular, more or less branched, tubular green filament. One of the most striking characteristics is the almost complete absence of cross walls except



Vaucheria. (A and C) Two species with oögonia, each containing an egg (o), and curved antheridia (a), with numerous sperms. (B) Plant showing branches, two of which have zoöspores.

at the time of reproduction. In fact, such cross walls as may be found in vegetative filaments practically always cut off diseased or injured parts.

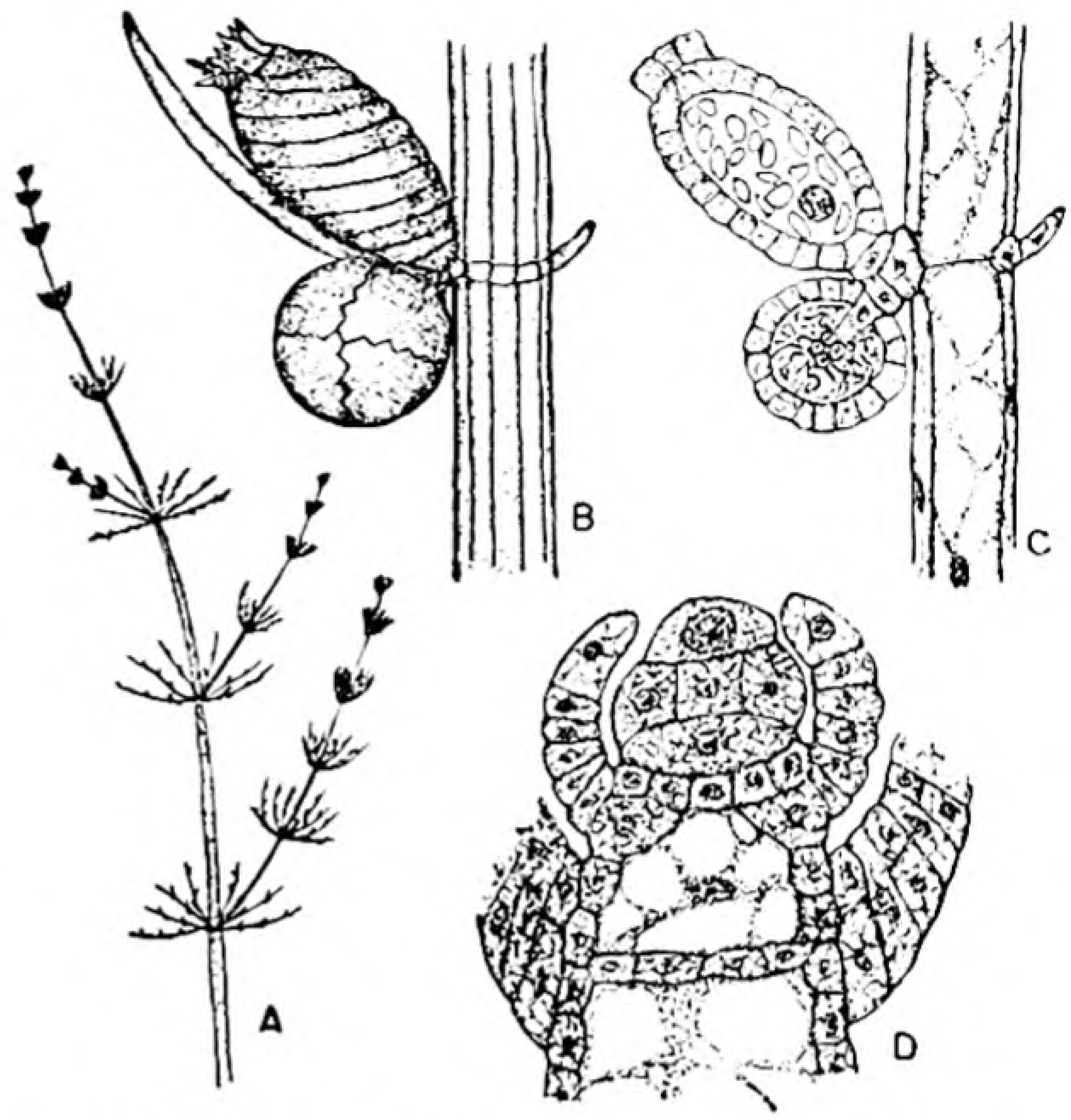
The chlorophyll is located in numerous round or elongated chloroplasts. Rapidly growing tips of filaments are sometimes almost colorless because the chloroplasts have not had time to develop.

REPRODUCTION. When *Vaucheria* plants are moved to the laboratory or when there has been some other abrupt change in their surroundings, they may reproduce asexually. In this process the end of a filament is cut off by a cross wall, an opening appears at the tip, and the rounded mass of protoplasm which has developed hundreds of flagella in the meantime, comes out as a gigantic, multinucleate zoöspore. This may be thought of as a compound zoöspore, for each nucleus has associated with it a pair of flagella, and the entire structure with its numerous nuclei only carries out the general coenocytic character of the whole plant. The zoöspore has ability to swim in water but in time stops moving and grows into a new plant.

Sexual reproduction involves the development of curved antheridia and rounded oögonia cut off by cross walls from the ends of very short, specialized lateral branches. Sperms are produced as usual and each swims by means of a pair of terminal flagella. The young oögonium has numerous nuclei, but these disintegrate until only one is left in the fully formed egg. The antheridium and oögonium often stand side by side on a filament, but in some species they are borne in complicated clusters. The sperm enters the oögonium by way of a special opening and fuses with the egg. The zygote undergoes a prolonged period of inactivity and germinates directly into a new filament. It seems probable that a reduction division takes place when the zygote begins to germinate.

Charales. These are peculiar green aquatic plants, very distinct from other green algae. Since *Chara* is the commonest representative and is thoroughly characteristic of the order, the following description of this genus also describes the order.

STRUCTURE OF CHARA. The *Chara* plant is composed of a slender, somewhat branched main axis that is anchored in the mud or sand by threadlike extensions known as *rhizoids*. These plants frequently form a compact growth in the water, like a tiny submerged forest a few inches tall. Along the



Chara. (A) Portion of a plant, about natural size. At each node there is a whorl of dwarf branches. (B) Stem with oögonium (*top*) and antheridium (*bottom*) at a node. (C) Similar stem as seen in longitudinal section. (D) Apical cell with nodes and internodes organizing from newly formed cells.

axis of each plant there are numerous whorls of short, horizontal branches, sometimes called "leaves." The main stem continues to grow indefinitely, but the smaller, whorled, dwarf branches soon stop growing, and all remain about equal in size.

Growth in length occurs only at the tip, by the division of a single *apical cell*. This growing region forms nodes and internodes alternately, the former producing the whorls of branches and the latter elongating.

At first, the internode consists of a single long cell, but this is soon reinforced by a cortex of filaments similar to the dwarf branches. One part of the cortex grows down from the node above and the other grows up from below.

REPRODUCTION. *Chara* has no zoöspores or other common asexual reproduction. When a plant is broken up, however, small pieces includ-

ing one or more nodes may behave much like cuttings of higher plants and produce new individuals.

Sexual reproduction involves some complicated structures. The oögonium is a single cell around which five dwarf branches grow spirally forming a cortex, thus following the general organization of the vegetative parts of the plant. The antheridium is a large, spherical structure many of the details of which are too complicated to be discussed here. It is sufficient to state that finally there are produced long chains of cells, each of which contains a sperm.

The zygote has the usual resting period but when it germinates it produces a juvenile plant only a few cells in length. This little resembles an adult *Chara* plant but from a node of it the adult plant arises.

A cluster of *Chara* plants usually feels harsh and stiff because of heavy deposits of lime compounds in the branches. As the plant grows, it takes dissolved lime out of the water and stores it in its cell walls. When it dies and decays, the lime is changed to a chalky deposit which sinks to the bottom. When a luxuriant growth of *Chara* has persisted in one place for a long period of years, this material, which is known as *marl*, may accumulate to the depth of many feet. *Chara* is unable to grow in regions where the water is "soft," that is, free from lime.

Summary. The red, brown, and golden algae, discussed in the last chapter seem not to be directly ancestral to the higher, more specialized groups of plants. Both the peculiarities of pigmentation in each of these and the forms taken by their food reserves give support to this conclusion. (See the chart on p. 200.)

In contrast with these divisions, the Protochlorophyta have the same chlorophyll-carotinoid complex that is characteristic of all the higher, more specialized green plants. Likewise, the food reserves of the green algae are largely of the same nature as those of the grasses, trees, and other important vegetation that covers the greater part of the land surface.

It seems, therefore, that ancient Protochlorophyta were probably the primitive ancestral forms from which the various modern green plants evolved. In later chapters there will be discussed many additional evidences that support this theory.

SUPPLEMENTARY READINGS

Smith, "Cryptogamic Botany," Vol. I.
Smith, "Fresh-Water Algae of the United States."
Tilden, "The Algae and Their Life Relations."

Chapter 16

MYCOPHYTA: FUNGI

Mycophyta comprises a group of plants of only distantly related classes thrown together to form this division of the plant kingdom and having in common only a total lack of chlorophyll. All fungi live either as parasites or as saprophytes. Their source of nourishment therefore is much like that of animals.

This is such an immense assemblage that only a few samples can be studied. These have been chosen from the four great classes belonging to this division.

The outline of the chapter follows:

- General Structure
- Myxomycetae
- Phycomycetae
- Ascomycetae
- Basidiomycetae
  - Hymenomycetes
  - Gasteromycetes
  - The Rusts
  - The Smuts
- Origins of Fungi
- Parasites and Scavengers
- Lichens
- Mycorrhizas

Fungi are plants that are somewhat like algae but which do not have chlorophyll. Mushrooms and molds are well-known examples. Because of the absence of chlorophyll they cannot carry on photosynthesis and therefore must derive their food from outside sources. In other words, they must nourish themselves directly or indirectly from green plants. Fungi that use dead plant or animal bodies, or the excreta or other wastes from animals, are known as *saprophytes*, and the material on which they grow and from which they get nourishment is called the *substratum*. By contrast, a fungus, as well as any other organism which absorbs food from a living plant or animal, is known as a *parasite*, and the organism which supplies the food is termed its *host*.

General Structure. The actively growing bodies of fungi vary in structure from single cells to free moving masses of protoplasm and to well-organized threads of definite cells. The filamentous nature of the molds and mildews is evident, and a microscopic examination of the large fleshy forms shows that they, too, are made up of tangles of threads so closely interwoven as to give the appearance of a solid structure.

The mass of filaments which make up the body of a fungus of the usual type is known as *mycelium* (*mykes*, fungus). This is a collective term generally having no reference to individual threads. A single fungal filament is called a *hypha*.

There are four classes of fungi distinguished from each other by structural and reproductive

differences. They are: *Myxomycetae* or slime molds, *Phycomycetae* or algalike fungi, *Ascomycetae* or sac fungi, and *Basidiomycetae* or club fungi. In addition to these definite groups there is a rather vague assemblage called the *Fungi Imperfecti* whose life histories are either unknown or are lacking in some step that would be necessary to place them with one of the main groups.

MYXOMYCETAE

Organization and Activities. The group of organisms commonly called slime molds and ordinarily known technically as *Myxomycetae* (*myxa*, slime; *mykes*, fungus) is very difficult to place satisfactorily in relation to other living things. These organisms are usually inconspicuous and are seldom noticed except by students. At one time in the life history of most of them they somewhat resemble other types of fungi, and at another they are very much like primitive animals.

The animallike phase of the life history occurs in the form of a soft, slimy mass of protoplasm known as the *plasmodium*, growing in or on many kinds of organic substances. In size, plasmodia range from those that are very small up to some that have an area as large as the palm of the hand. Rotten logs and stumps, old sawdust piles, and masses of decaying fruit, such as the pomace from cider mills, are common habitats, but some species are to be found on or within living plants. Colors of whitish or yellow are most frequent, but even green may be found although the pigment is not chlorophyll.

Plasmodium of myxomycete creeping over the ground near decaying stump.

Plasmodia are able to move by a slow irregular flowing motion. In this way they may travel for considerable distances through and over their food supply or, in laboratory experiments, even over sheets of glass or other materials which cannot be used in their metabolism. They take up solid pieces of food of various kinds as they move about. These food particles are surrounded by the protoplasm and are subjected to digestive action. Undigested parts are left behind as the plasmodium moves away. All this action is definitely animallike.

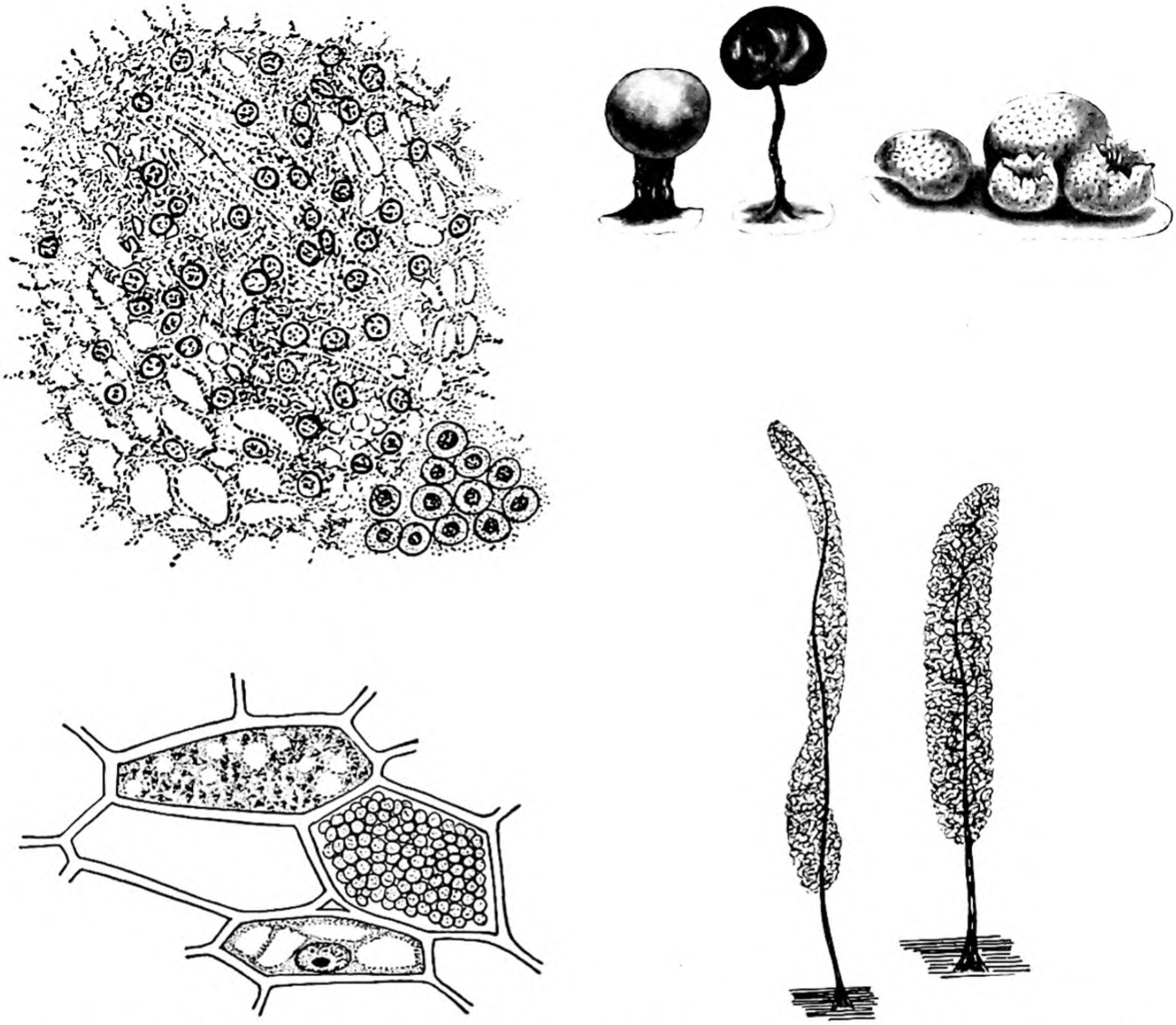
The movement of a plasmodium is so coördinated that elaborate designs of branching and anastomosing streams may be formed. A microscopic examination of a moving strand shows that the motion is not continuous. Instead, a flow of several seconds in one direction is followed by a shorter one in reverse, so that progress is really made by a series of pulsations.

Microscopic examination of stained sections shows that the plasmodium consists of vacuolate cytoplasm containing numerous scattered nuclei. In other words, it is a complete coenocyte.

If conditions are not suitable for the continued activity of the protoplasm, it may form a hard, dry, horny mass, known as a *sclerotium*. The sclerotium occasionally remains dormant for some time, only to resume activity as a plasmodium on the return of conditions favoring growth.

When the time comes for a plasmodium to change to the fruiting phase, it first makes a radical change in its reaction to light. As a vegetative mass it has a negative response, hiding away in cavities in its substratum, or remaining in deep shade. Now, however, it comes out into the light and creeps over such solid objects as may be in its path. It is at a time like this that the plasmodium is most easily observed.

In the production of sporangia, the cells, which have behaved as independent individuals, except for their coördinated movements, act together in building a remarkably specialized structure. The



Myxomycetae. (*Top, left*) Plasmodium with scattered nuclei and, at the lower right, forming spores, as seen in sections. (*Bottom, left*) Cells from cabbage with club root, a disease caused by a slime mold. Upper cell containing plasmodium; cell to the right, containing spores; normal cell of root at bottom. (*Top, right*) Characteristic sporangia of slime molds. (*Right*) *Lycogala.* (*Left*) *Trichia.* (*Bottom, right*) *Stemonitis.* Showing stalk surrounded by the capillitium.

method varies with the different genera, but, as an example, in *Stemonitis* a small portion of the protoplasm first elevates itself in the form of a short, stiff stalk, and then more of the material flows up over this stalk and organizes a more or less elongated mass on top. This becomes more firm, and each nucleus, with a small portion of the cytoplasm, becomes surrounded by a cellulose wall, forming a spore. The left-over dried network of cytoplasm forms the framework of the sporangium, called the *capillitium,* and the spores sift out at maturity. In some other genera the sporangium assumes the form of a low, flat structure without a stalk, that is made up almost entirely of spores. Some of the commonest representatives of this simple type are to be found among the species of the genera *Fuligo* and *Lycogola.*

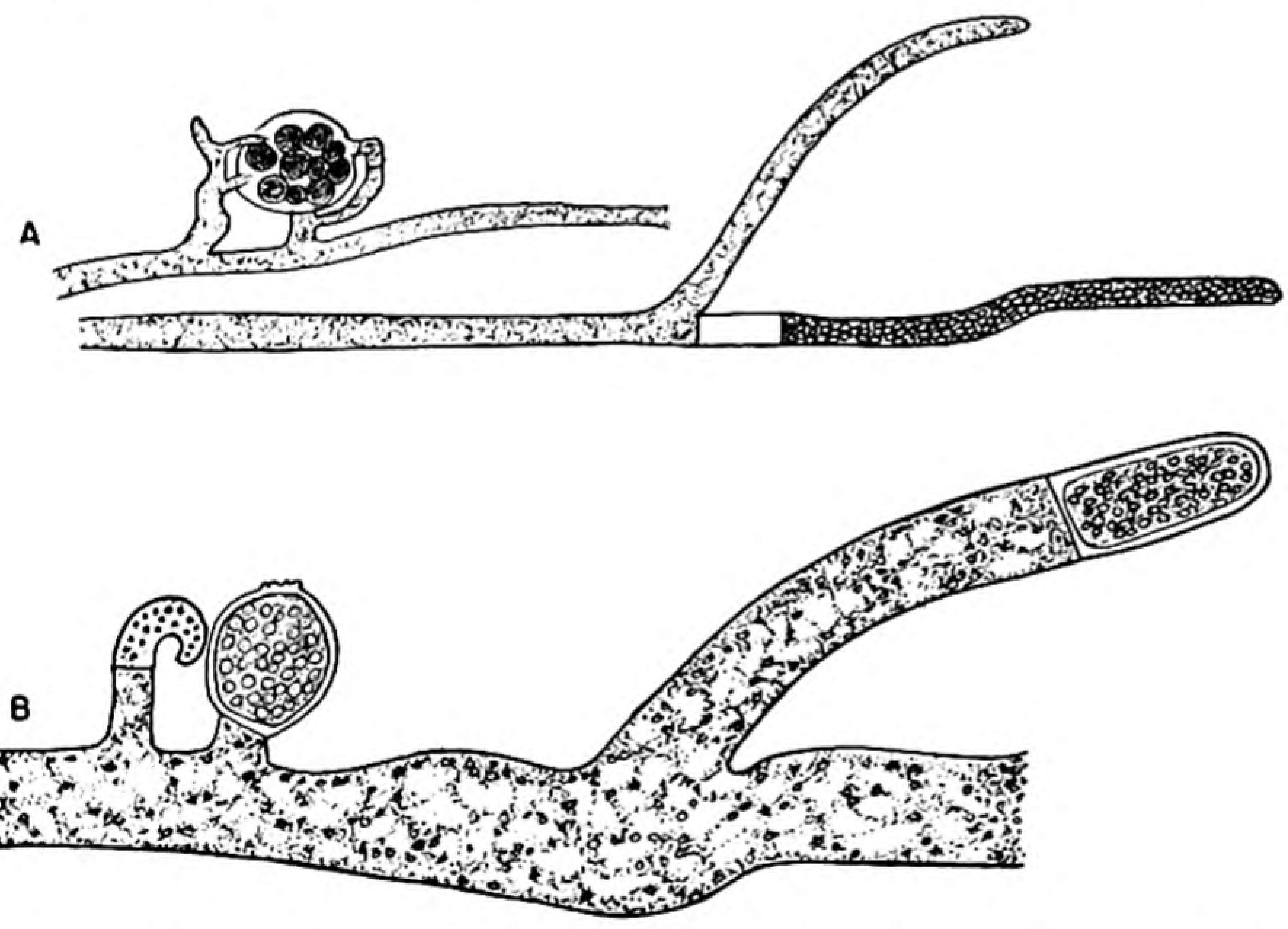
The Life History. By no means all steps in the life history of the various genera of *Myxomycetae* have been investigated, but the parts that are known can be pieced together, giving a series which seems to be fairly reliable. A reduction di-

vision occurs at the time the spores form. They have, therefore, the *n* or gametophyte number of chromosomes. When they germinate, each produces a small naked cell which appears, under the microscope, much like one unit of a plasmodium. As these protoplasts take food and grow, they undergo a series of divisions and transformations during a part of which time they often develop a single terminal flagellum. In some species at least, these swimming cells finally unite in pairs, forming zygotes. The zygotes germinate without a reduction division, giving rise to small amebalike cells which flow together, making little plasmodia whose nuclei divide mitotically and whose protoplasm increases in amount with the assimilation of food. Beginning with the zygote, the *2n* or sporophyte generation continues until reduction division occurs in the production of spores.

Relationships. The slime molds are so animallike in such a large number of respects that some biologists are inclined to class them entirely in the animal kingdom. As the formation of spores with cellulose walls is distinctly a plant characteristic, these organisms should probably be considered to be closely related to those forms near the dividing line between animal kingdom and plant kingdom. In other words, these plant-animal organisms may be thought of as being not far removed from certain parts of the Chrysophyta; or perhaps they are related to the *Euglena* group of Protochlorophyta.

PHYCOMYCETAE

The Phycomycetae are the algalike fungi (*phykos*, alga; *mykes*, fungus). Some of them are very much like certain green algae and may have originated from them by the loss of ability to produce chlorophyll and by a few other changes. The fact that almost all Phycomycetae are coenocytic (that is, their filaments are not divided into uninucleate cells by means of cross walls) while all other filamentous fungi are more or less completely septate (that is, the cells are separated from each other by cross walls) indicates a possible origin of the Phycomycetae from coenocytic Protochlorophyta. This view is strengthened by the great similarity between *Vaucheria* and the water molds to be discussed in the next paragraphs.



Saprolegnia and *Vaucheria*. (A) *Saprolegnia* with oögonium containing eggs, and antheridia with sperms. (*At right*) Sporangium filled with zoöspores. (B) For comparison, the green alga, *Vaucheria* with similar reproductive structures in similar positions.

Water Molds. These fungi take their common name from the fact that a great many of them live in water, deriving their food from dead plants and animals, or sometimes acting as parasites on aquatic animals. In addition, some species are known to live saprophytically in the soil.

The genus most often studied is *Saprolegnia*. This fungus is a branched coenocyte, reminding one of *Vaucheria* (p. 226.) The filaments of *Saprolegnia* are much smaller in diameter than are those of *Vaucheria* and of course the fungus has no chloroplasts. In most other respects the two are remarkably alike.

Good growths of *Saprolegnia* can often be secured by leaving dead flies or other insects in a vessel of ditch or pond water for a few days. Success depends on the presence in the water of

reproductive cells of the fungus. When a good growth occurs it forms a whitish zone, made up of radiating hyphae, around the body of the insect.

REPRODUCTION. These fungi reproduce asexually by zoösporelike cells, biciliate in some species. As in *Vaucheria* they form in the tips of filaments and become set off from the main plant body by means of a cross wall behind them. The most important differences lie in the fact that in *Vaucheria* a single giant coenocytic zoöspore develops in a filament while in *Saprolegnia* numerous uninucleate ones organize.

There is a great deal of variation in the details of sexual reproduction in the different species of *Saprolegnia*. The antheridia and oögonia usually form on short branches along the sides of the main filaments much as in *Vaucheria*, but instead of swimming sperms, *Saprolegnia* has nonmotile ones that are carried directly to the eggs by fertilization tubes extending from the antheridia to the oögonia.

In some species antheridia are rarely produced and fertilization does not occur. The eggs, however, develop into zygotelike structures and complete the life cycle without fertilization having taken place. The growth of an unfertilized egg into a new individual as if fertilization had occurred is called *parthenogenesis*.

The water molds are characteristically saprophytic, but a few are parasitic. At least one species attacks the head and gills of living fish. These animals soon die, but there is some question as to how much of the damage should be charged to the fungus and how much to unfavorable conditions of some other kind which first lower the vitality of the host and make it susceptible.

Black Molds. This is a small group of algalike fungi with black spores that float as living dust particles in the air. The common name, black mold, comes from the fact that when the spores are being formed in large numbers the myriads of near-microscopic sporangia give a blackish or grayish appearance to the entire mycelium. Probably the best known representative of this group is the common bread mold (*Rhizopus nigricans*), which can be found almost everywhere on moist, stale bread, or decaying bananas, pumpkins, or potatoes. It appears as a weft of white filaments over the surface of any substratum on which it grows, and an attempt to pull the latter apart shows that it is thoroughly reinforced with a tangled mass of mycelium.

There seems to be no essential difference between the mycelium inside the substratum, commonly called the rhizoids, and that spread over the outside except that the former is much more irregular in size and shape and much more branched. Both kinds of mycelium consist of long, tubular filaments with no indication of a division into separate cells except in the places where reproductive structures are being produced. The cytoplasm is gray and granular in appearance, and the nuclei are small and numerous. In portions of the mycelium which are growing rapidly, a streaming movement of the cytoplasm may be observed, the movement being in the direction in which the filament is growing.

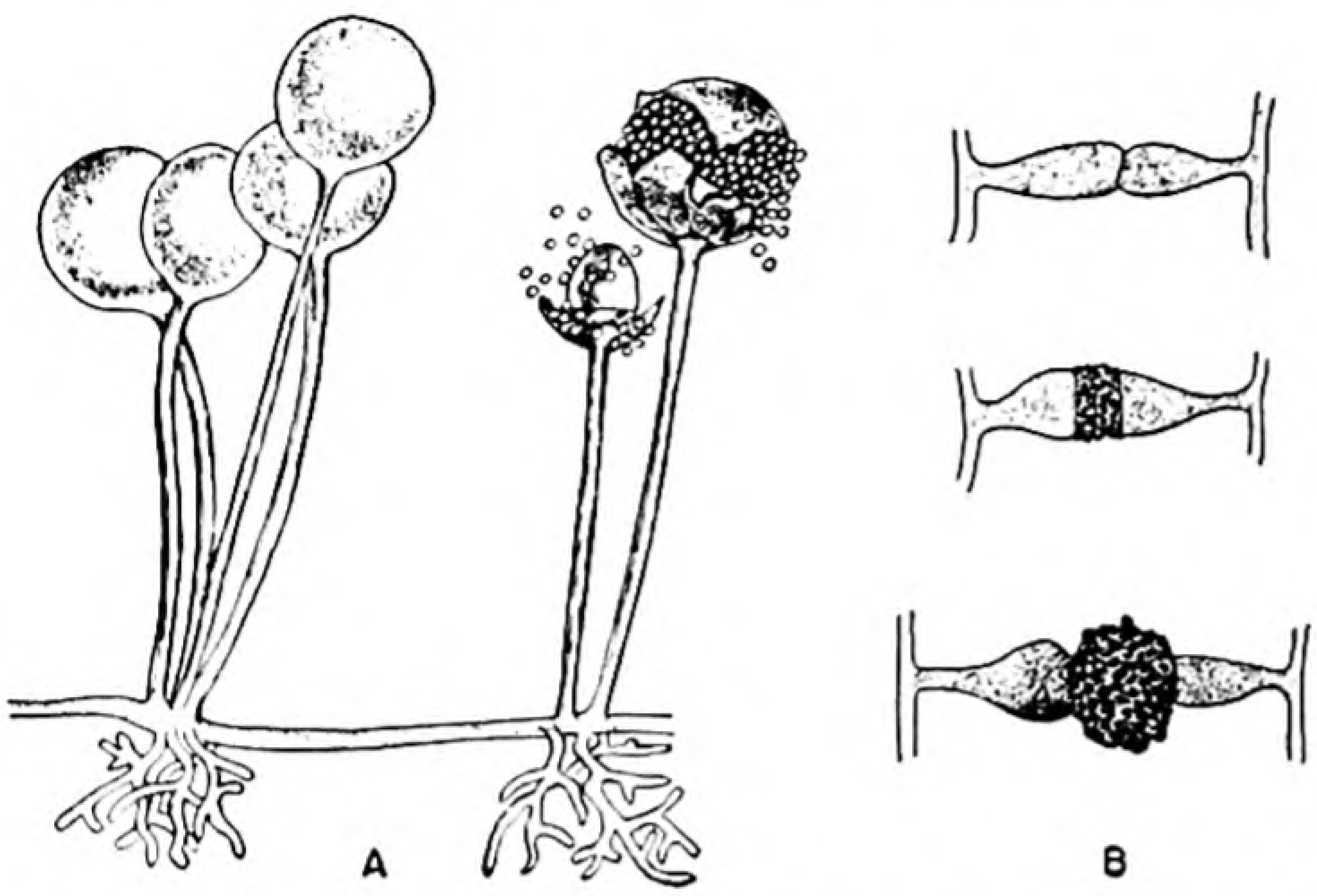
This tubular type of mycelium, which gives to the entire plant body the form of a single complicated coenocyte, again recalls the structure of such algae as *Vaucheria*.

ASEXUAL REPRODUCTION. The mycelium on the surface of the bread or other substratum usually grows rapidly, extending the fungus over large areas and into new supplies of food. A much more definite type of reproduction is brought about with the formation of asexual spores. In the latter process the end of an aerial hypha comes into contact with the substratum, attaches itself by rootlike holdfasts (rhizoids) and sends up a vertical shoot on the end of which a sporangium is formed.

The sporangium is at first a globular enlargement containing cytoplasm with a large number of nuclei. As development proceeds, a dome-shaped wall forms, separating the inner framework, the *columella*, from the spore-producing portion which surrounds it. The latter separates into a large number of cells, each containing several nuclei. These multinucleate cells finally become brown or black spores. Enormous numbers of them may be formed by a small amount of mycelium, and at maturity the wall of the sporangium breaks and they float away in the air. On making contact with a suitable substratum, they germinate immediately and produce a new growth of mycelium. Under favorable

conditions the complete cycle from spore around to spore again may take place within two or three days.

These spores are produced in such abundance that in homes, in grocery stores and bakeries, and in laboratories where the fungus is grown occasionally for study, the air is never entirely free of them. To secure a culture of the fungus at any time, it is usually only necessary to expose a piece of bread to the air for a few minutes and then to keep it in a moist, warm place for two or three days.



Rhizopus. (A) Horizontal hypha with developing sporangia (two with spores) (*above*) and rhizoids (*below*). (B) Stages in conjugation.

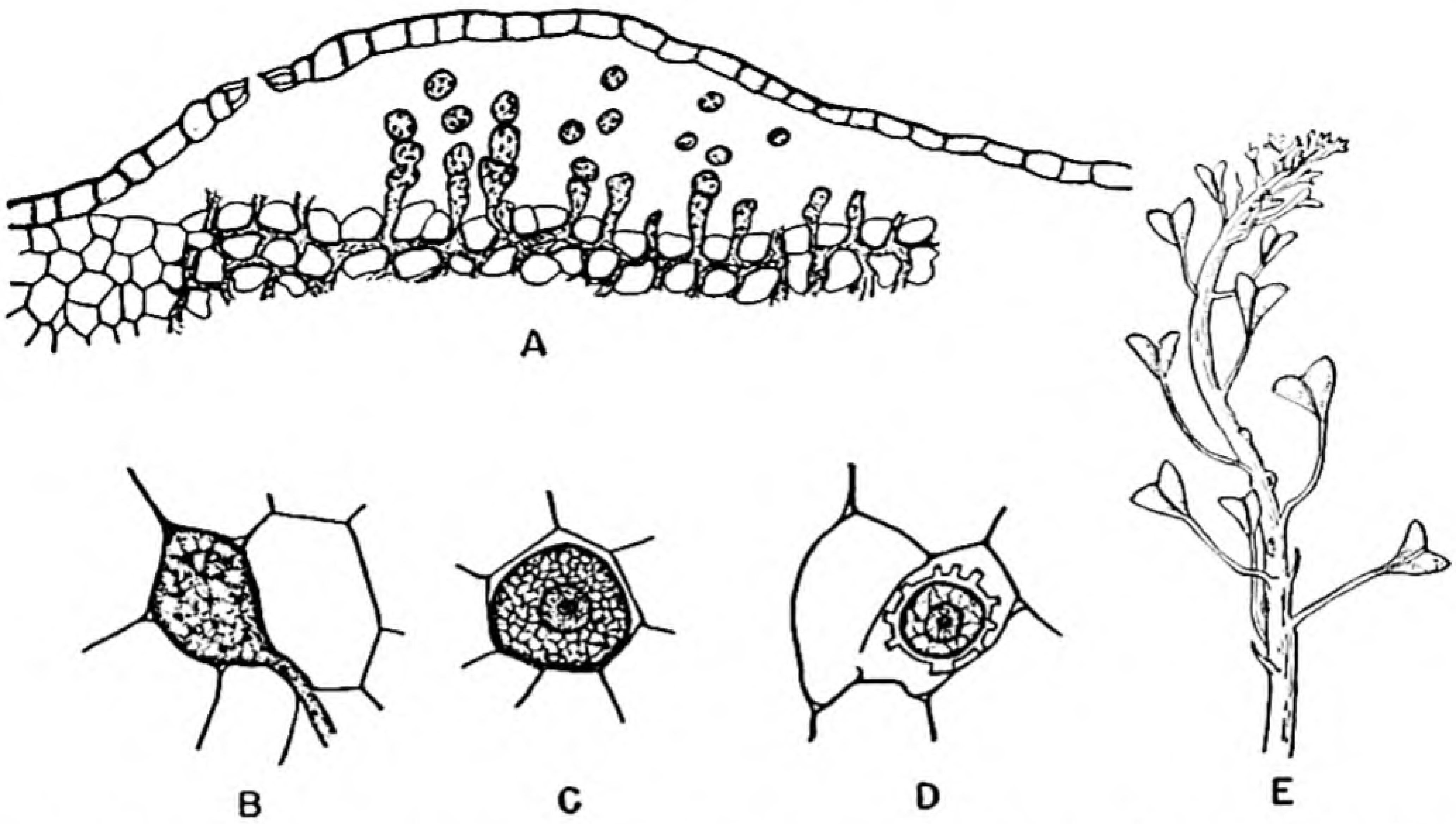
SEXUAL REPRODUCTION. Bread mold has, at times, a kind of sexual reproduction which somewhat suggests that of *Spirogyra*. Thick, club-shaped hyphae, produced on separate plants, meet in pairs. A multinucleate gametic cell, densely gorged with cytoplasm containing large numbers of nuclei, is cut off by a cross wall near the end of each. The walls between the two gametes dissolve, allowing the two masses of protoplasm to flow together. The nuclei of *Rhizopus* are extremely small and microscopic observation of their behavior in conjugation is still incomplete. Some students of the subject have thought that they observed nuclear pairing but others are in doubt. At the end of the process a thick, dark wall, marked externally by warts or ridges, is formed around the whole. This multiple zygote shows the usual resistance to adverse conditions. Under favorable circumstances it germinates, producing a short piece of hypha which bears a single small sporangium. The spores that form in it germinate, giving rise to new mycelia.

When ordinary bread mold is grown in cultures produced naturally, zygotes are seldom formed. A number of unsuccessful attempts were made to discover the secret of zygote formation before it was found, about 1903, that in bread mold and in some other species, slightly different strains of mycelium were necessary for conjugation. It is now known that the two uniting gametes and the plants on which they form are sexually different. The female plants are sometimes called + strains, and the males, − strains. In nature, one of the sexes is much more prevalent than the other and zygotes therefore often fail to be formed. Under these conditions reproduction takes place entirely by asexual means.

Parasitic Phycomycetae. The most important group of these fungi with nonseptate or coenocytic mycelia consists of a number of genera which live only as parasites, chiefly on plants. Some of the hosts are crop plants, and the diseases caused by the fungi bring about great economic losses. Various common names are applied to these diseases and to the fungi causing them, but the latter are essentially molds in character.

The "White Rusts." The genus *Albugo* is responsible for the disease known as white rust on a number of kinds of plants, including purslane, amaranths, sweet potatoes, morning-glories, and many members of the mustard family. This so-called rust is really a kind of mildew and should not be confused with the true rusts which occur on the cereals and many other plants. The true rusts belong to an entirely different group, the Basidiomycetae, and are not at all closely related to the Phycomycetae.

The species, *Albugo candida*, which lives on the common weed known as shepherd's purse, a member of the mustard family, is typical of the group. The disease makes itself known usually after early spring rains, by a distorted



Albugo. (A) Section through "blister" showing conidia forming under epidermis of host, and hyphae among cells of cortex. (B, C, and D) Stages in formation of egg and rough-coated zygote. (E) Plant of shepherd's purse with numerous "blisters."

enlargement of the stems, leaves, or fruits of the host, and by the appearance of white blisters.

Microscopic preparations show the branching, tubular filaments of the fungus in the spaces between the cells of the host. Usually the only places where host cells are penetrated by the hyphae are where short, knoblike branches known as *haustoria* extend through the cell walls where they absorb food. Because of this behavior of the mycelium, this fungus does not kill the host but seems, rather, to stimulate its tissues to an overgrowth which results in the deformities by which the diseased plant is recognized.

Reproduction. In certain localized spots numerous hyphae, crowded close together, grow outward until they reach the epidermis. From the end of each of these, numerous small, round, white, aerial spores, known as *conidia*, are cut off. It is the accumulation of the conidia in these places which raises the epidermis, forming the white blisters on the stems and leaves. These blisters break open, and the conidia are distributed by the wind. Each conidium contains a number of nuclei, usually five or more, and when it falls on the wet surface of its proper host, it first germinates and produces as many zoöspores as it has nuclei. Each zoöspore swims about by means of a pair of lateral flagella for a few hours in the film of moisture but finally comes to rest and develops a filament which may penetrate host tissues and produce a new infection.

Sexual reproduction is similar to that in the water molds. Deep in the tissues of the host, usually in the parenchyma of the stem, antheridia and oögonia are formed from the ends of hyphae. In the oögonium, a large egg develops from a coenocytic mass of protoplasm. But by the time it is mature it contains only one of the many nuclei, the others having disintegrated. The antheridium produces a fertilization tube which penetrates the outer layer and allows a nucleus to enter and unite with that of the egg. The zygotes remain in the tissues of the host until liberated by decay or mechanical disruption during the winter. In the spring, when the young seedling host plants have begun to grow, the zygotes of the fungus produce a crop of zoöspores which swim to the host and renew the infection.

Late Blight of Potato. The fungus *Phytophthora infestans* causes the very destructive late blight of potatoes and similar diseases on a few related plants. Attacking the growing plant, the mycelium quickly makes its way through all the parts. The stem and leaves die, and many of the potato tubers

decay in storage, if not in the ground before they are dug. When infected tubers are planted, the disease is transmitted to the next crop. Under conditions favorable for the fungus the disease spreads very rapidly and is extremely destructive. The great famine in Ireland in 1845 has been attributed, in part, to this disease, and many less serious crop failures have had a similar cause.

The rapid spread of the disease in damp weather is brought about by conidia which are produced in great numbers on clusters of long, branched filaments thrust out through the stomata of the host. The conidia produce zoöspores, as in *Albugo*, before infecting the host. Sexual reproduction is similar to that in *Albugo*, with minor variations in the structure and arrangement of the oögonium and antheridium, but in most cases the oögonium produces a zygotelike structure without the aid of sperm, that is, it is parthenogenetic.

Grape Mildew. The "downy mildew" of grapes is caused by another fungus of this group, *Plasmopara viticola*. The common name is suggested by the downy appearance of the conidiophores on the surface of the host. This name might as well be applied to *Phytophthora* also, but the blighting effect on the host has taken precedence in naming that parasite. The mildew causes the grapes to rot and also does considerable damage to the young stems and leaves.

This fungus seems to have had its origin in America, on wild grapes or Virginia creeper. Although it does serious damage to these hosts, and to cultivated grapes developed from wild American species, it proved to be much more destructive to the wine grapes of Europe after it had gained entrance into France in 1878. The accidental discovery, in the vineyards near Bordeaux, of the effectiveness of a copper sulfate spray in preventing the disease, led to the perfection of the Bordeaux mixture, which is now widely used as a fungicide.

ASCOMYCETAE

These fungi range in size and structure from the microscopic single cells of yeast to one of the edible mushrooms, commonly known as the morel.

As the naked or almost naked plasmodium is characteristic of the Myxomycetae, and branched coenocytic filamentous hyphae are peculiar to Phycomycetae, so the *ascus* (plural, *asci*) is the most marked single feature of the Ascomycetae. The ascus is, characteristically, a peculiar enlarged tip of a hypha, containing eight spores. There are numerous deviations from this standard pattern, such as larger or smaller numbers of spores, but usually these variations are obviously only minor modifications of the basic type.

Ascomycetae, and Basidiomycetae as well, assume many forms. A few of them are single-celled individuals, others develop thin growths of tangled, cobweblike hyphae, and still others organize close-knit mycelia that may take on a more or less firm and fleshy structure. The conspicuous, fleshy parts of the latter are almost always associated with the production of spores.

The student who for the first time is studying fleshy fungi of any kind, is likely to think of the *sporophore*, that is, the spore-producing body, as constituting the whole fungus. Nevertheless, the greater part of the plant is almost entirely hidden in the substratum. Such a mycelium may be seen frequently as an extensive system of white branches on the surface of the wood, when loose bark is pulled from dead trees or decaying logs in a forest. The slender fungal threads secrete enzymes that digest the wood, changing it to soluble substances. The fungus absorbs this food and is, therefore, able to continue to live and grow. When the mycelium has become mature and when weather conditions are suitable, a spore-producing structure, the *sporophore* or *sporocarp* is organized.

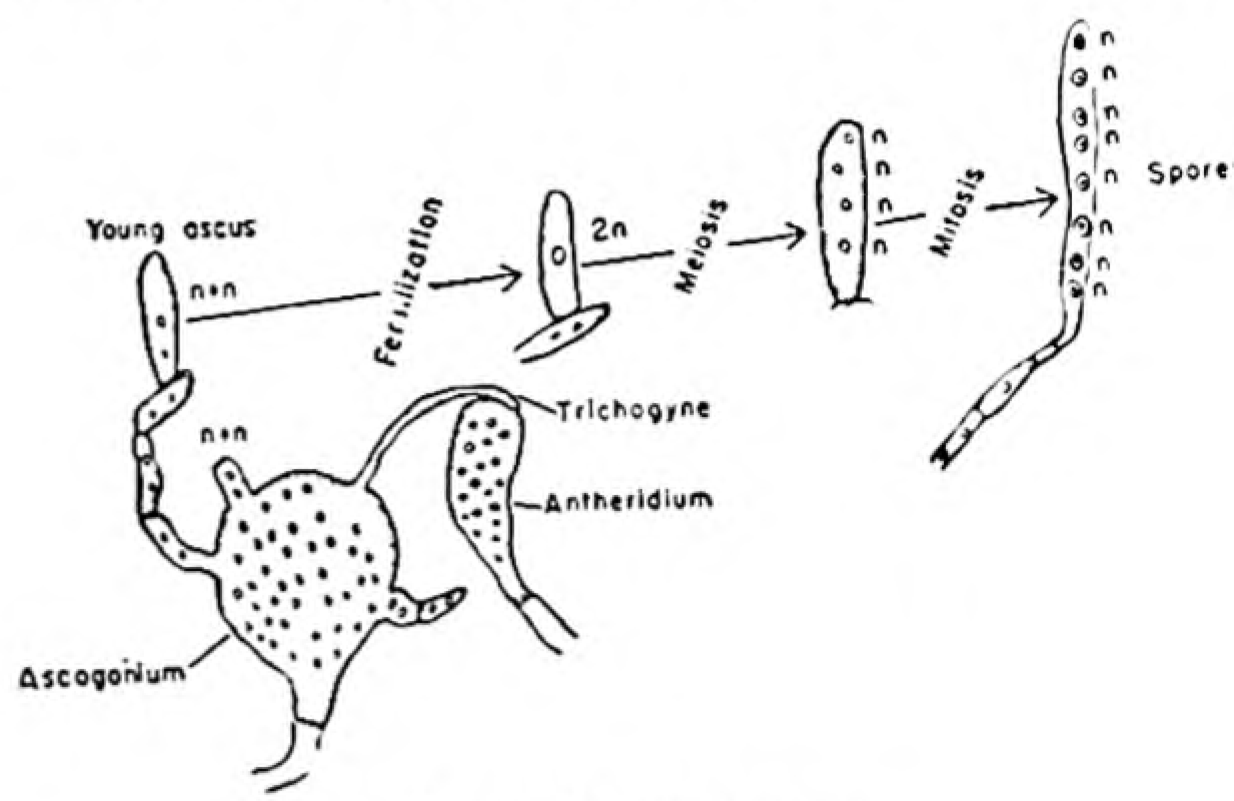
Cup Fungi. Among the more conspicuous of the fleshy ascomycetes found growing on rotten logs or decaying leaves in forest soils are several kinds with cup-shaped or flat, disklike fruits. Specialized spore-bearing structures of Ascomycetae are called *ascocarps* (*carpon* fruit).

Among the most common of these are several species belonging to the genus *Peziza*. The cup is usually lined with a bright orange or red color, although in some cases it is brown. *Peziza* is characteristically so fragile that it must be handled with great care to avoid damage. This is in reality

a very complicated sporophore. The diameter may vary from one to several centimeters.

The lining of the cup or the covering of the upper surface of the disk of these ascocarps is a layer known as the *hymenium*. It is composed of a large number of long, slender asci together with many similar but narrower sterile filaments known as *paraphyses*. When an ascus with its eight ascospores becomes mature it may explode with such force as to send the spores a short distance into the air. On picking up one of these fruits to examine it, one is sometimes startled at seeing what seems to be a puff of smoke suddenly rising from it, the effect being produced by the simultaneous ejection of spores from the many thousands of asci when the plant is disturbed.

There is a remarkable difference in ascus formation in the various fungi of this group. A study of the development of some of the Ascomycetae of this type, however, shows that this is an involved process. Both plus (female) and minus (male) hyphae must be present. In the region where the hymenium is about to organize, one or several oögonia, commonly called *ascogonia*, take form at the tips of hyphae. Each one becomes a spherical body containing numerous nuclei. Extending from its outer end is a trichogyne. At the same time, branch tips on male hyphae become club-shaped multinucleate antheridia. The trichogyne curves around an antheridium whose numerous nuclei enter and find their way to the ascogonium. Aside from the fact the ascogonium and antheridium contain many nuclei, these structures remind one of the carpogonia and antheridia of red algae. It is difficult to follow the behavior of the numerous small nuclei from the two sources, but this much is clear: hyphae now begin to extend out from the surface of the ascogonium and two nuclei migrate into each hyphal cell as it forms. Any such binucleate cell is called a *dicaryon*. During growth both nuclei divide at the same time in any given cell, thus maintaining the binucleate condition throughout the hypha. Numerous branches form, and eventually specialized tips give rise to young asci, each with its pair of nuclei. These two fuse as if they were gametes, giving rise to a single diploid nucleus. This peculiar zygote divides meiotically producing four haploid nuclei. Each of these undergoes mitosis, thus accounting for the eight nuclei in the ascus. A spore is formed when a wall and a bit of cytoplasm organize around each nucleus. The zygote, therefore, is the only cell



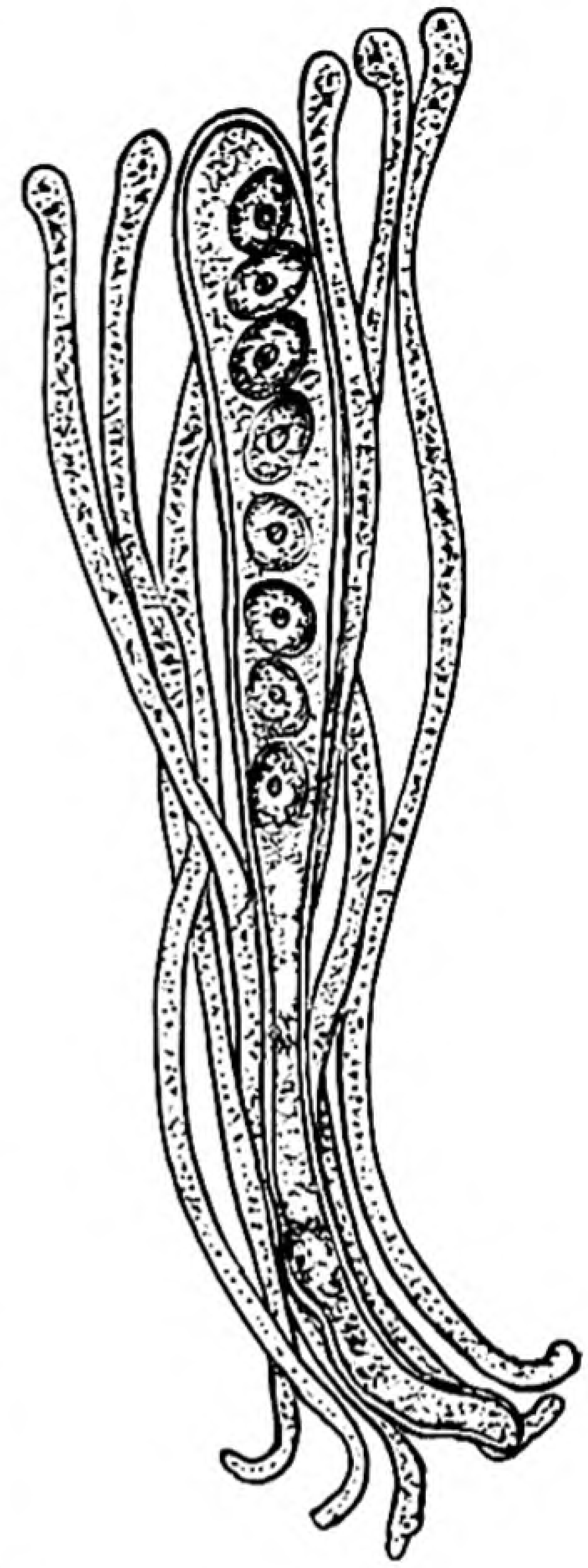
Ascus development.

with the diploid number. The vegetative parts of the fruit, including the paraphyses, and the mycelium in the substratum are all haploid.

Of the millions of ascospores produced in an ascocarp, almost all are lost. The few which reach a suitable substratum presumably germinate directly and develop a vegetative mycelium. The most exacting experimentation indicates that the sexes are set off from each other during meiosis. This accounts for the fact that half the spores develop into female hyphae and the other half into male.

THE MOREL. One of the finest of all edible mushrooms, the common morel, is really a kind of cup fungus. The numerous cavities in the enlarged upper parts are lined with hymenium, and the entire fruit may be regarded as a compound ascocarp. (See left cut on next page.) This structure is more evident in some of the less common species in which the fruit consists of only three or four cups.

Powdery Mildews. Any one who has observed the leaves on lilac bushes or willow trees in late summer has noticed a slight grayish coating on some of them. This filmy covering sometimes has much of the appearance of dried soap suds, but microscopic examination shows it to be the mycelium of a fungus. Such an examination may reveal the presence on the leaf surface of a light dusty coat of conidia. The resulting appearance is responsible for the common name, powdery mildew.

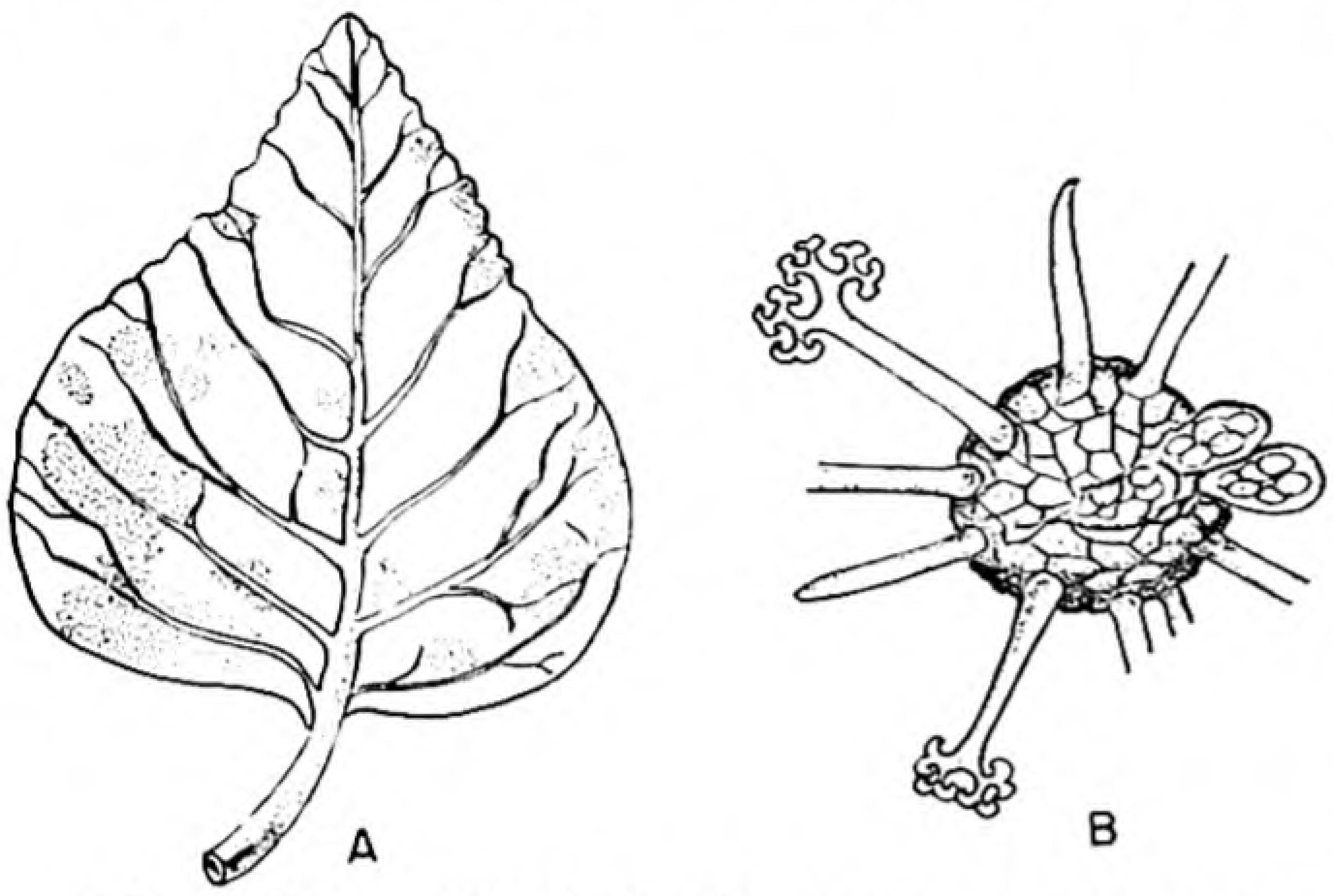


Ascomycetes. (*Left*) Ascocarps of morel. This fleshy mushroom is widely sought after because of its fine eating qualities. Its small cups are usually brown inside. (Courtesy, Bessey: "A Text-book of Mycology," Philadelphia, The Blakiston Company.) (*Bottom, right*) *Peziza*. Usually bright scarlet inside. (*Top, right*) An ascus containing eight spores; also six paraphyses. The hymenium is made up of asci and paraphyses.

There are numerous species of powdery mildews that grow on as many kinds of plants, including such well-known cultivated and weedy species as lilac, willow, cherry, oak, smartweed, rose, plantain, clover, dandelion, bean, hop, and grass.

The mycelium of the various species of these fungi is almost entirely external to the host, food being absorbed from the epidermal cells by extensions from the hyphae, called haustoria, which penetrate their walls. In a few species short branches extend deeper and absorb food from subepidermal tissues. Because of the superficial habit of the fungus, the host is not seriously damaged except when growing tips are attacked or when the blotches detract from the appearance of ornamentals, such as roses.

REPRODUCTION. Throughout the summer these fungi reproduce rapidly by means of conidia. These are oval or barrel-shaped spores cut off one by one from the upper ends of *conidiophores*, which are short branches of mycelium arising at right angles



Lilac mildew. (A) Leaf with numerous ascocarps. (B) One ascocarp highly magnified, showing protruding asci and several appendages.

to the surface of the host. They are scattered by the wind and, when they reach the proper host, they may germinate, forming hyphae on the epidermis.

At the end of the growing season, small, spherical, black fruit bodies appear on the mycelium as a result of a union of gametes. In most species these fruits bear a number of long, conspicuous appendages whose sharp-pointed, hooked, or dichotomously branched ends are helpful in identifying the various genera.

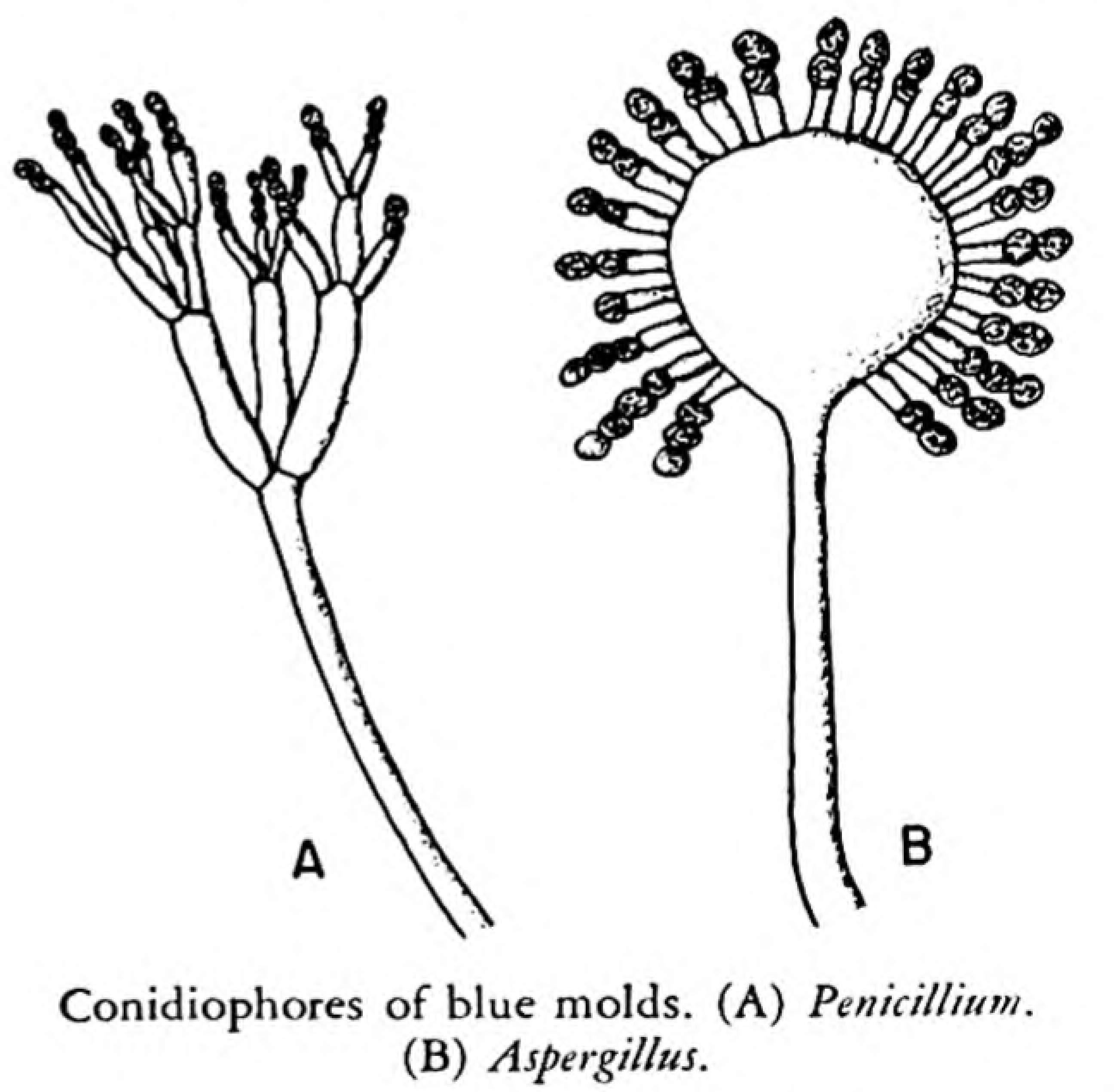
The ascocarp, sometimes called an *ascogonium*, has a hard, dark-colored wall enclosing one or more asci.

The details of fertilization and the subsequent development of the ascogonium are complicated and not easily observed, but certain facts should be recognized. The asci develop from a short row of cells which grow out more or less directly from the fertilized egg. The wall of the fruit, however, is formed by the ordinary vegetative mycelium which is in some way stimulated by the growth of the tissue resulting from fertilization, so that it grows up around the developing asci, reminding one somewhat of the development of cystocarps in some of the red algae. When they are mature, the asci contain the ascospores.

Although there is some variation from species to species in the details of sexual reproduction in Ascomycetae, their life histories can readily be correlated with the typical one involving the alternation of generations. The vegetative mycelium and the conidia are haploid, and the fertilized egg and young asci before the spores are formed constitute the diploid tissue. Reduction division occurs during the formation of the ascospores.

The Blue Molds. Some of the blue, green, or black molds which occur on many foods such as cheese, canned fruit, and jelly, and the mildews on leather and soiled clothing are very similar to the powdery mildews. Their conidiophores frequently branch in a manner characteristic of the species and produce an abundance of conidia. The ascocarp varies in the different species but always produces the characteristic asci, following a sexual fusion of nuclei.

Two of the commonest forms of these molds are the genera *Aspergillus* (*aspergillum*, a rounded brush used to sprinkle holy water) and *Penicillium* (*penicillus*, pencil, referring to a pencil brush used in writing, etc.). Reference to the drawings of the



Conidiophores of blue molds. (A) *Penicillium*. (B) *Aspergillus*.

conidiophores of these genera will make evident the basis for the names.

Within the last decade the name *penicillin* has come to be well known throughout the civilized world. It was first discovered and named as a prod-

uct of *Penicillium notatum*, then a wild species. Now, thanks to the combined efforts of numerous investigators, new and prodigiously productive strains have been developed that can be grown under completely controlled aseptic conditions. These valuable, highly cultivated forms are grown in 10,000-gallon tanks under the supervision of highly trained scientists and technicians. Such specialized factories are widely scattered throughout the world, producing the great quantities of penicillin required to control many of the most serious infectious diseases of humanity.

Other cultivated species of *Penicillium* give the characteristic odors and flavors to the different kinds of cheese. The dark lines often seen in the freshly cut surfaces of some of these are layers of conidia.

Other Ascomycetae. The ascomycetes make up a large and complicated group of fungi, and it is impossible in an elementary presentation to treat such an assemblage at all thoroughly. The types already discussed give some idea of the life history of the main subdivisions. A few more species may be mentioned because of their conspicuousness or because of some noteworthy characteristic.

ERGOT. The disease known as ergot is found on a number of the cereals and on many wild grasses, but it is probably best known on rye. As the rye plants are maturing, the diseased condition becomes manifest by the development of large black structures where the grains would be expected. These consist of the overgrown framework of a rye grain thoroughly permeated with the dried mycelium of the fungus. A hard, dry mass of mycelium like this is known as a *sclerotium*.

The sclerotia fall to the ground and remain dormant until spring, when each forms one or more small, but conspicuous, pink or purple sporophores, each consisting of a rounded head on a stalk, with asci produced in numerous cavities. The long, slender ascospores may be carried by the wind to young rye flowers, repeating the infection.

The mycelium coming from the ascospores and growing on rye next produces abundant conidia which may infect other rye plants. The conidia are carried about chiefly by insects which are attracted by a honey-like liquid secreted by the mycelium. After a brief period of conidia production, the mycelium passes into the dormant sclerotial condition.

The chief interest in ergot is not in any destructive effect that it may have on the host plant—for

Head of rye with sclerotium of ergot replacing a grain.

that is seldom of much consequence—but in the poisonous nature of the sclerotia. Cattle and other animals having access to rye straw sometimes eat enough of the fungus to suffer serious consequences. In extreme cases hoofs become sore and loosened, tails and ears fall off, and calves may be lost by abortion. This fungus is particularly injurious to dairy cattle.

People have been poisoned at times by eating bread made from grain that has not been carefully freed from sclerotia. Such poisonings have been almost entirely limited to European peasants during times of food shortage. It should be understood that standard milling methods in the United States make rye flour safe from all such dangerous contamination.

Ergot is the source of a valuable drug that is used in a variety of ways in medical practice, being especially effective in reducing hemorrhage, and in bringing about the contraction of the uterine walls at the time of childbirth.

YEASTS. Much that was said in Chapter 13 about the chemical activities of bacteria and about the methods used in studying them, is also true in a general way of the yeasts. The latter are so different in structure, however, and are so evidently not closely related to the bacteria that they merit separate consideration.

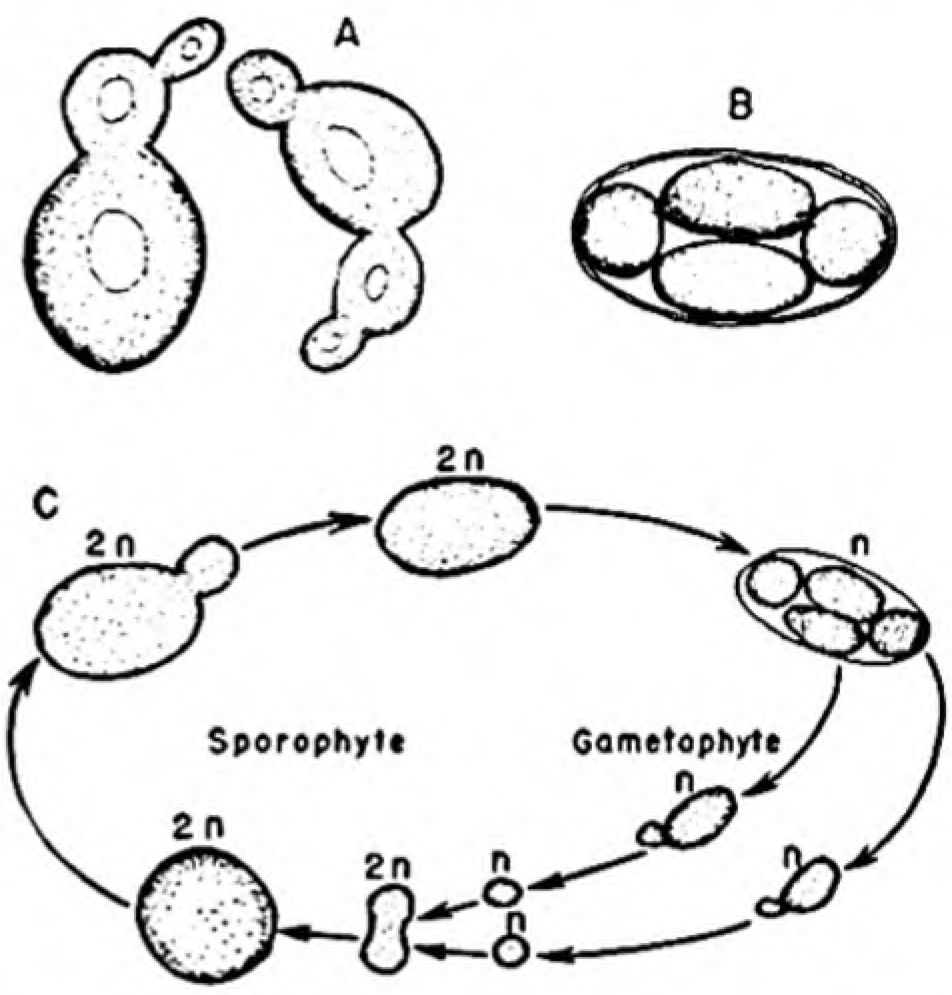
Like bacteria, yeasts are abundant in the air almost everywhere. Besides the cultivated species used in baking and brewing, there are many wild forms which are responsible for at least the first steps of the fermentation and decay of many organic materials, and a few are known to cause human diseases.

Most species of yeast grow best in solutions that contain a large amount of sugar or of some other carbohydrates which can be changed readily into sugar. In utilizing it as a source of energy the plant breaks it down into carbon dioxide and alcohol by means of enzymes (see p. 48).

The individual yeast plant is a single cell. In most species the cell is globular or oval in shape. Occupying the center is a large vacuole, and lying within the cytoplasm that surrounds the vacuole is a small nucleus.

The most common form of reproduction is a peculiar kind of cell division known as budding. In such divisions a small, wartlike inflation is pushed out on one side of the mother cell, the nucleus divides, apparently without organizing chromosomes, one of the new nuclei moves out into this "bud," the daughter cell breaks off, and the division is complete. The newly formed cells often remain attached for some time to the older ones, producing irregular chains.

Within recent years it has been discovered that, in addition to budding, which is an asexual form of reproduction, such species as the common bakers' yeast (*Saccharomyces cerevisiae*) also have a life cycle that includes gametic union. The ordinary cultures of this yeast are diploid. Under certain conditions, a diploid cell may give rise to four spores enclosed within its wall, in this way becoming a simple, primitive ascus containing four haploid ascospores. Each of these ascospores is capable of producing a small yeast plant which can reproduce itself by repeated budding. These buds act as gametes that unite in pairs. While there is no visible distinction between the offspring from the different spores, there is a slight sexual distinction. This difference is shown by the fact that certain of the gametes unite readily and successfully while



Yeast. (A) Budding yeast cells. (B) Yeast cell with four ascospores. (C) Life history of brewer's yeast.

others do not. The outline of this life history shows that bakers' yeast is a true ascomycete with a sexual stage that is only slightly removed from isogamy (see p. 215).

BASIDIOMYCETAE

This class of fungi includes such well-known forms as the mushrooms, puffballs, rusts, and smuts. In all members of the group there are spore-bearing structures called *basidia* (singular, *basidium*). Basidia are very similar to asci in both structure and function. The most obvious difference is that basidiospores are produced on the exterior of the basidial hyphae while the ascospores are formed in the interior of asci. Also, there are characteristically only four spores developed by each basidium instead of the usual eight in the ascomycetes.

Probably the best known of all the basidiomycetes are the more conspicuous members of the mushrooms and their relatives, the bracket fungi. These represent the subclass, Hymenomycetes.

Hymenomycetes. These fungi take their name from the fact that their spore-producing struc-

tures form definite layers which, as in the ascomycetes, are called *hymenia*. In all the Hymenomycetes there are layers of exposed basidia so placed that the spores are shed directly into the air. The umbrella-shaped mushrooms, familiar to almost everyone, belong to this group. There are many species of these, ranging in size from some that are almost microscopic to others more than a foot in diameter. They grow in a great variety of places, representatives being found in almost any habitat which affords them a food supply. Almost all are saprophytic, living chiefly on humus and decaying logs, leaves, and manures.

GILL FUNGI. One of the commonest kinds of hymenomycetes has a number of radiating gills hanging from the cap. An examination of this type will lay a foundation for an understanding of the whole group.

As in the cup fungi, the part ordinarily seen is only the spore-producing structure, or *sporophore*, which is an outgrowth from an extensive system of mycelium distributed in the substratum. The cap technically known as the *pileus*, is borne on a stalk, the *stipe*, and bears on its lower side the gills, or *lamellae*. The hymenium covers both surfaces of each gill. In many species a ring of tissue known as the *annulus* is around the stipe some distance below the pileus. It represents the place where the edges of the pileus were attached to the stipe while the young mushroom resembled a closed umbrella. In some species the bottom of the stipe is set in a cuplike structure, the *volva*, which is in reality the remains of a wrapping which originally enveloped the entire stipe and pileus before they expanded.

A dissection of any part of the mushroom shows it to be made up of hyphae so closely massed together as to resemble the nonfilamentous tissues of the higher plants. The hymenium consists of the greatly enlarged end cells of filaments which have turned outward into such a position that they

Mycelium of fungus on decaying log.

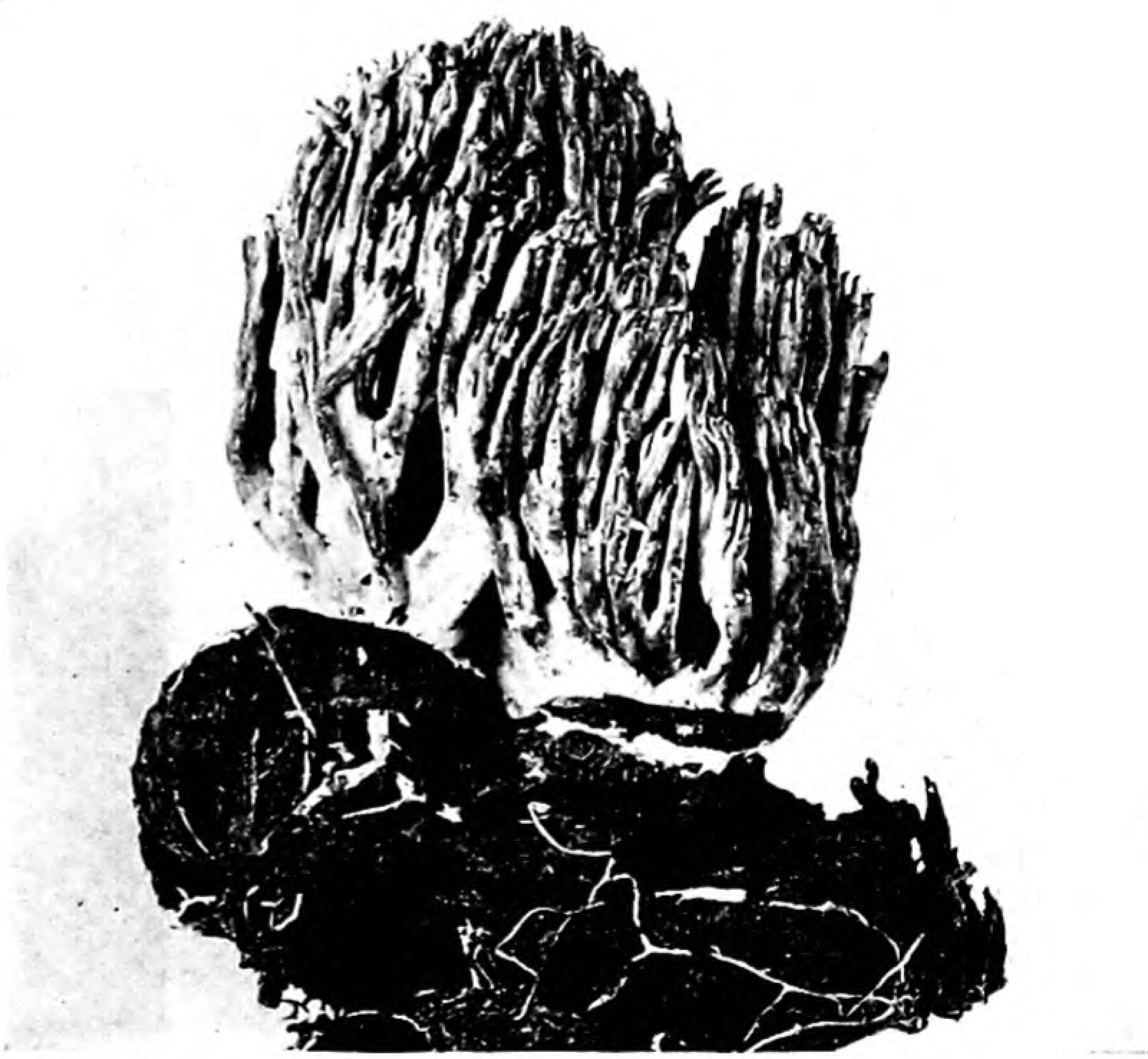
stand at right angles to the body of the gill. Certain of these long cells of the hymenium are the *basidia*. In most species each basidium bears four external *basidiospores*, each one of which is supported by a slender stalk known as a *sterigma* (plural, *sterigmata*). At maturity each spore is shed, falling free of the gill, where it may be carried away by the wind.

Probably no more than a very small fraction of the spores ever germinate, and only a few of these succeed in establishing a mycelium in a suitable substratum. How long the mycelium grows before another spore-producing structure appears is not well known, but after a time it accumulates in masses in suitable places, and a rounded "button" is produced below the surface of the substratum. Unless the weather is unusually moist these buttons may remain dormant for a long time, but following a rain they absorb water and enlarge without much cell division. Growth of this kind is usually so rapid that it is proverbial that mushrooms spring up suddenly after a rain. They do appear suddenly, but it should be understood that they are already formed and have only to imbibe water in their colloidal bodies and expand.

OTHER HYMENOMYCETES. The sporophores of the different genera and species vary a great deal in shape. In some of the umbrellalike species the hymenium is the lining of numerous small canals or pores in the lower surface of the pileus, while in others it forms a covering over finger-like or toothlike projections. (See cuts at right.)

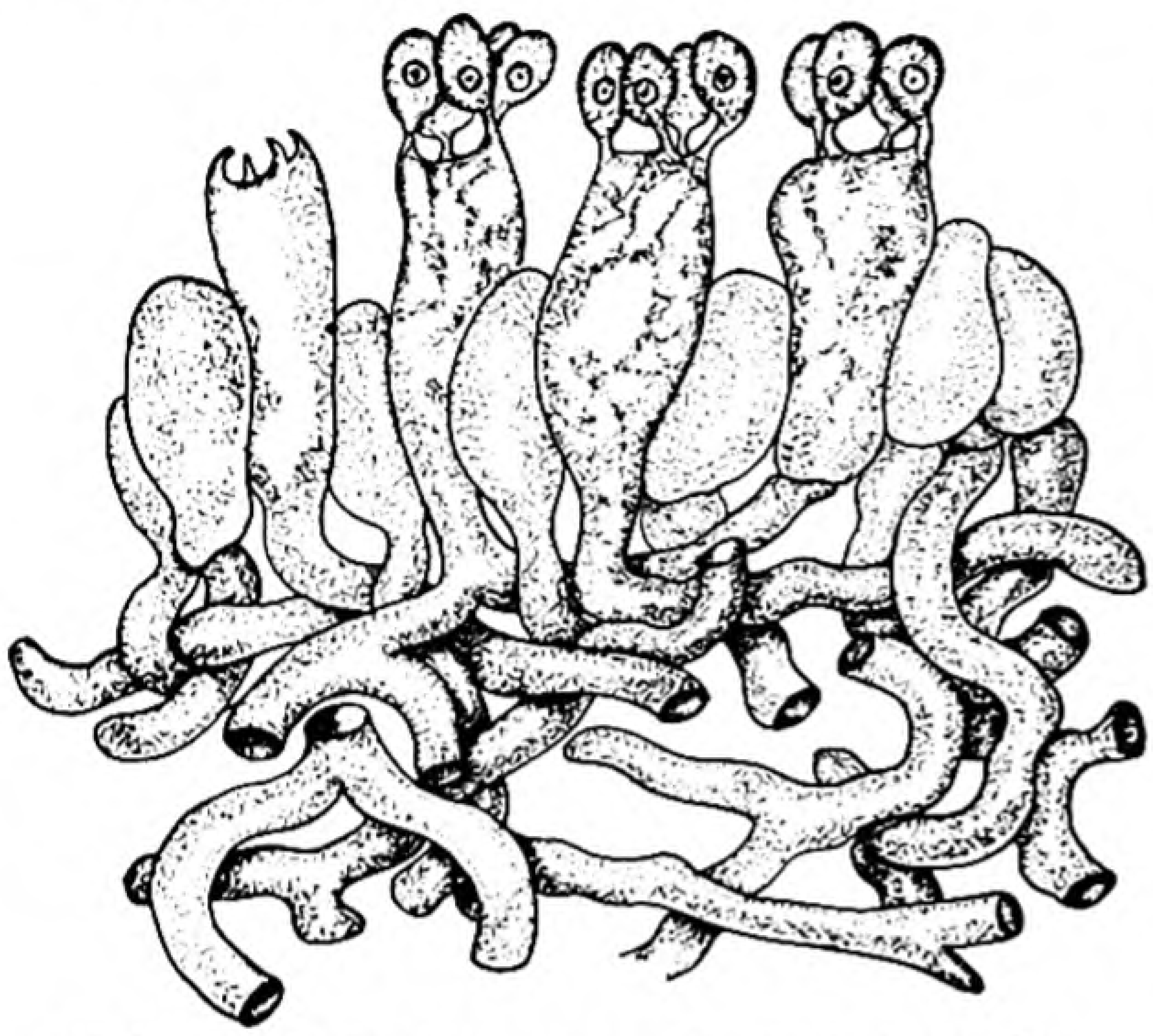
Another form of sporophore is the familiar "bracket" so often seen on stumps and logs in the woods. The different genera and species of these have gills, pores, and teeth, much like those of the umbrella type. Many of the bracket fungi become hard and woody, producing new hymenial layers under the old ones from time to time over a period of several months or even years.

In still other genera the hymenium takes the form of shallow pores, teeth or gills on the surfaces



Hymenomycetes (*Top, left*) Gill fungus showing pileus with gills, supported on the stipe. Just below the pileus is a ring of tissue, the annulus, and at the bottom is the cup or volva. (*Top, right*) Pore fungus showing pileus with numerous pores, supported on stipe. (*Bottom*) Coral fungus. (*Bottom*, courtesy, National Museum of Canada, Ottawa, Canada.)

of mycelia that grow firmly attached to dead branches or other decaying woody surfaces; and in some Hymenomycetes, the spore-bearing surface is smooth and regular.



Club-shaped basidia, three of which have four basidiospores each.

Gasteromycetes. The common puffballs, some type of which is known to almost everyone, belong to a group known as *Gasteromycetes* (*gaster*, stomach) which differ from the Hymenomycetes in having their spore-producing mycelium completely enclosed, stomachlike, by vegetative tissue. In all of these the basidia form a more or less definite lining of irregular open spaces inside the fleshy body. Puffballs vary in size from a fraction of an inch to 18 inches in diameter.

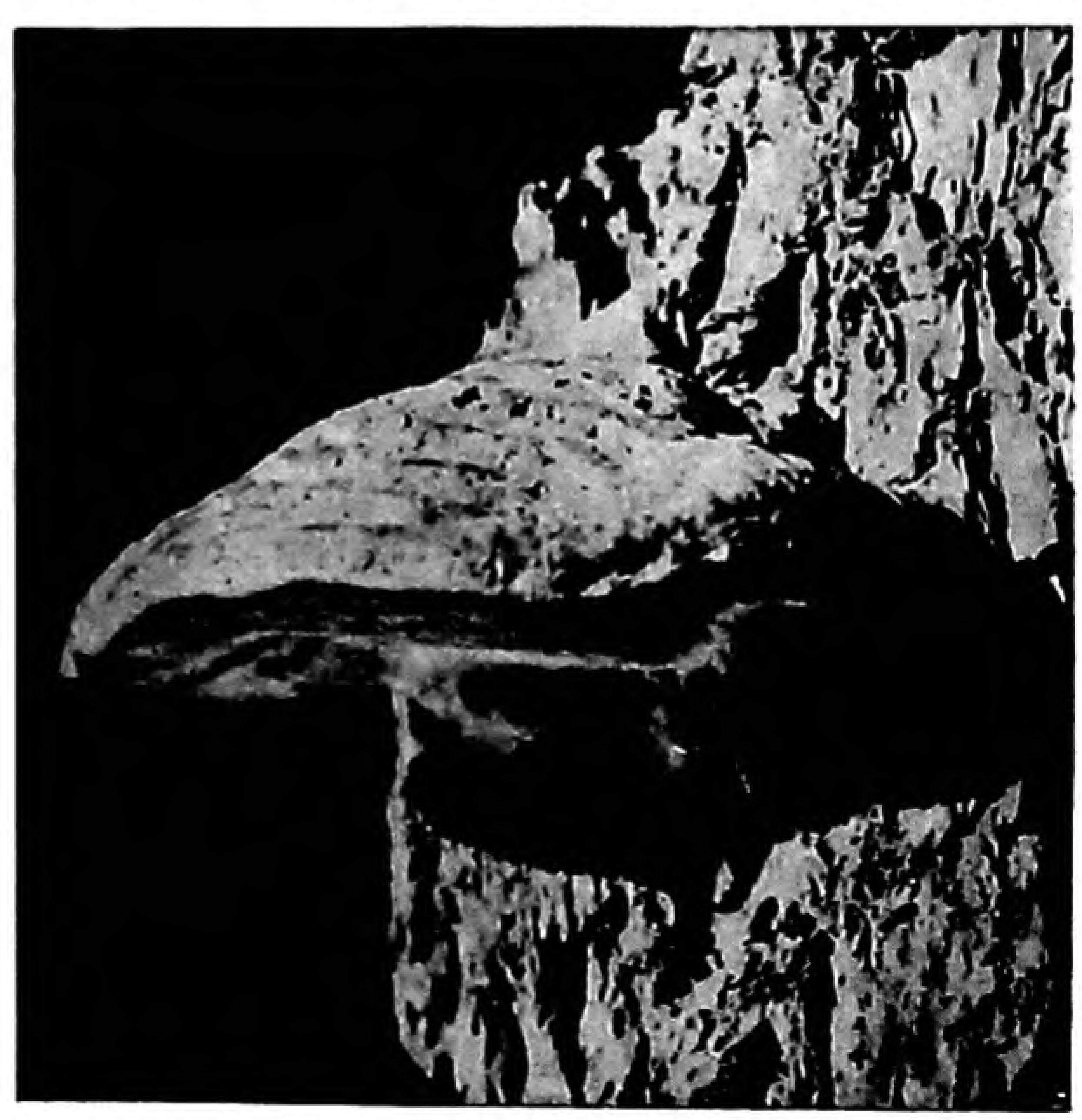
The young puffball is firm and white throughout, but as the spore-bearing layer develops, the tissues darken and become softer and drier. At maturity the outer wall or walls break open in a way characteristic of the particular species, and the covering acts like a bellows, puffing out the brown spores when it is touched.

One kind of puffball has a fleshy or leathery outer covering which splits into five or six segments at maturity. The common name, geaster (*geo-*, earth; *aster*, star), comes from the star-shaped figure formed by these reflexed segments. At the same time an inner layer covering the sporogenous tissue opens at the top, and the rest of the story is much like that of any other puffball.

A few other fungi somewhat similar to the puffballs are interesting curiosities. One of these is the "stink horn" which takes its name from its foul odor. The young sporophore resembles a puffball with a double covering over the spores. At maturity, an axis elongates into a stalk, which carries the spore-bearing portion up into the air, while the torn covering remains at the base, forming a cup. The spores, instead of being dry, are surrounded by a dark, slimy substance which is responsible for the smell. Flies attracted to this odor carry away the slime on their bodies and thus spread the spores. The many species of stink horns may be found in forests or on lawns. (See left cut on p. 246.)

The bird's nest fungus is another modification of the puffball type. There are several species which can be found on decaying wood or on soil rich in humus. The sporophore body is usually more or less funnel-shaped. At maturity a sort of cap splits open at the top of the funnel, disclosing four to six rounded bodies in which the spores are produced. At this time the whole structure resembles a tiny bird's nest full of eggs. The spores are shed much as in the case of the true puffballs.

Life History. The life cycle of hymenomycetes and probably of gasteromycetes is fundamentally



Bracket fungus on bark of dead tree.

Puffballs. (*Top*) Group of small sporophores. (*Bottom*) Hymenium surrounding irregular open spaces, as seen with the microscope.

similar to that of the ascomycetes described above. Here again the mycelium develops from haploid spores which are sexually distinct. By a complex series of steps nuclear exchanges occur when the male and female hyphae come in contact with each other. In this way numerous dicarya are produced without the intervention of antheridia and oögonia. After a period of growth, the young basidia form much after the manner of young asci. The two nuclei of the young basidium unite only to undergo meiosis with the formation of four haploid nuclei. These migrate into the sterigmata and form the external spores.

It becomes evident, with all these facts in mind, that the binucleate cells of the mycelium including the sporophore, should be thought of as belonging to the sporophyte generation. Likewise, the fusion of these two nuclei in the young basidium is a peculiar type of fertilization. Reduction division seems to follow fertilization at once, and the spores belong to the gametophyte generation. This generation continues until the binucleate stage is reached in the developing mycelium.

The Rusts. The fungi commonly known as rusts are extremely important from two very different points of view, the one being economic and the other technical. The destructive effects of some of these fungi on the cereal crops are easily seen and are well known, and many others play a prominent, though less spectacular, part in limiting the production of other economic plants. There are few fields in which the student of plant diseases has proved his worth in a more striking way than in devising methods for the control of these fungi. On the other hand, if they were of no economic significance, the rusts would still hold a prominent place in botany because of their peculiarly complicated life histories, their special relationships to their hosts, and the ways in which they are thought to be related to other fungi.

Many of the rusts have such extremely intricate life histories that long periods of time were required on the part of investigators to decipher them. Some of the most complicated of these cycles pass through a series of phases in which the fungus produces various kinds of spores and assumes more than one form, often attacking two kinds of host plants at different phases of the cycle. This type of behavior can best be made clear by means of sample life histories.

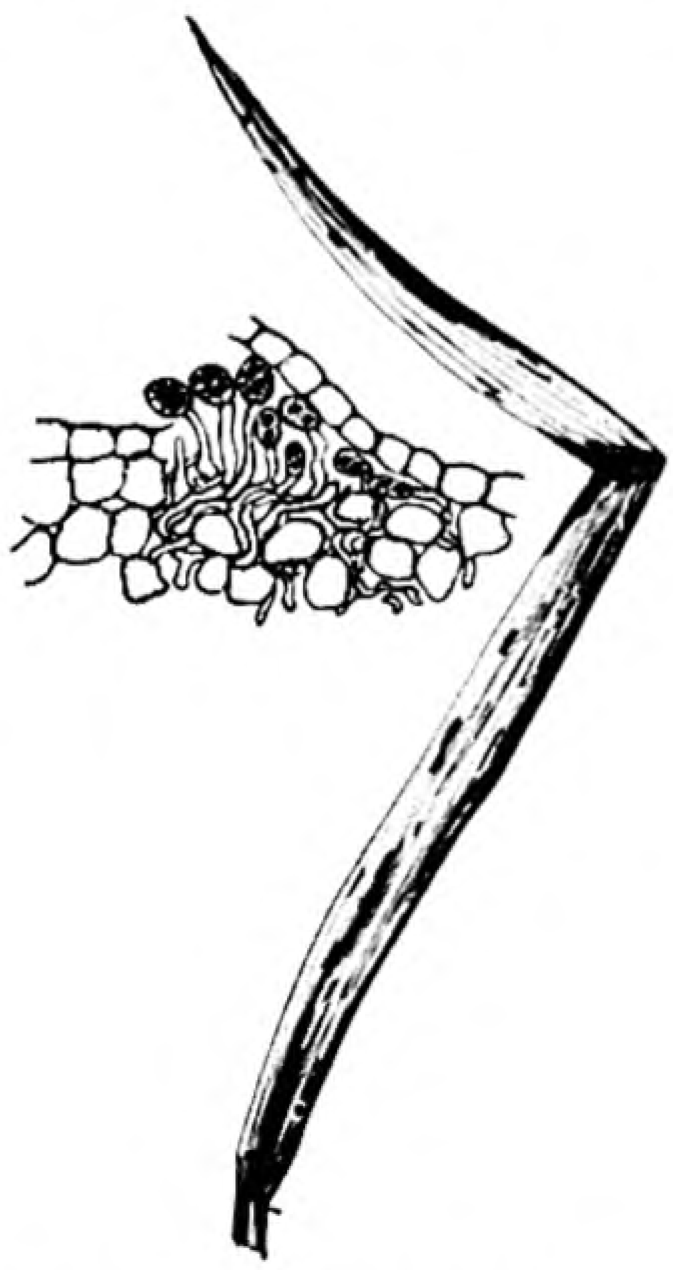
BLACK STEM RUST (*Puccinia graminis*). The destructive effects of stem rust on wheat have probably been known longer than those of any other rust. Although the nature of the fungus involved was not known, there are records which indicate that preventive measures were being employed against it at least 200 years ago. It is still being extensively studied, both by those interested in the growing of grain and by those primarily concerned with fungi.

Different forms of this rust are found on a number of grasses, but the life history followed here will be principally the one that occurs on wheat.

UREDINIAL PHASE. One who walks through a wheat field at harvest time frequently finds his

Other *Gasteromycetes*. (*Left*) Earthstar. (*Right*) Stink horn.

shoes covered with a reddish dust. This dust consists of the spores of wheat rust. A close examination of the wheat plants reveals bright brownish stripes made up of untold thousands of these spores breaking through the epidermis of the leaves and stems (see cut on this page). Farmers long ago observed the resemblance between this dust and iron rust. The fact that the most noticeable development often came in wet weather strengthened the comparison, and many persons who have had no opportunity to learn of the part played by the fungus, have assumed that moisture affected the wheat plants directly just as it caused rust to form on an iron or steel farming implement which had been left exposed. This peculiarity of spore color has given the name *rusts* to a large group of closely related species, many of which, however, do not produce reddish spores.



Uredinial stage of wheat rust, showing stripes of urediniospores on leaf; also epidermis of wheat broken by growth of spores as seen with the microscope.

The mycelium of wheat rust grows in the tissues of the affected plants for at least ten days before there is any evidence that they are infected. Then spores in large numbers begin to break through the epidermis. The mycelium causes the death of some of the cells of the wheat plant, in this way interfering with photosynthesis and metabolism in general. In addition, the numerous breaks in the epidermis occasioned by the emergence of the spores permit excessive transpiration and the consequent drying of the tissues of the host. For these reasons diseased plants usually do not yield as much plump, well-matured grain as do those that are not affected.

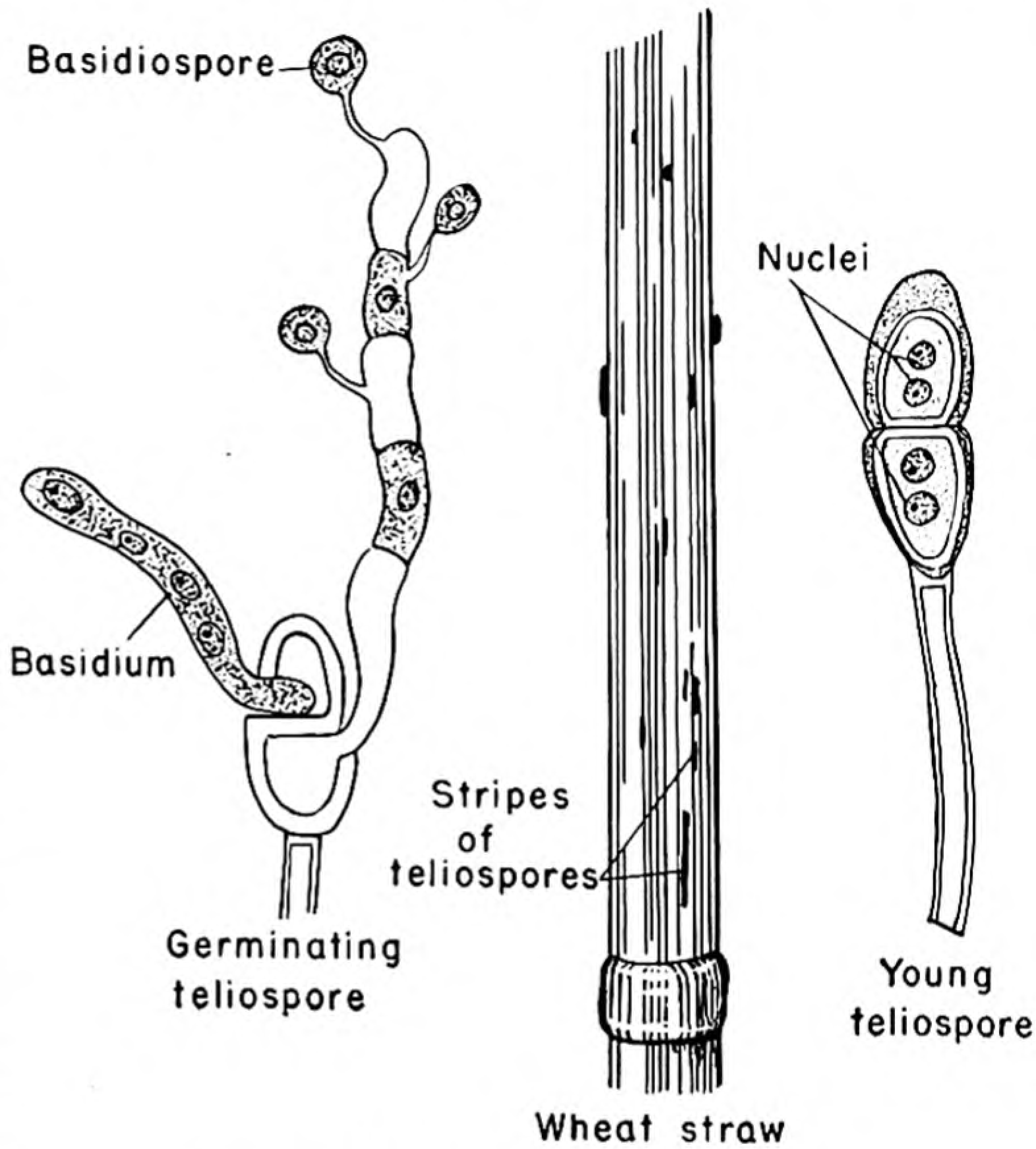
These rust-colored spores are known as *urediniospores*. Each one consists of a single cell containing two nuclei. The wall is somewhat thickened, except at a thin place through which a hypha emerges when the spore germinates. Urediniospores are scattered by the wind. When they are being shed in large numbers, especially when weather is moist and is in other ways suitable to promote prompt germination, they bring about a rapid spread of the disease from plant to plant and from field to field. These spores can infect only a wheat plant or some closely related grass.

TELIAL PHASE. Somewhat later in the summer the mycelia produce another form of spores, the *teliospores*. These are especially numerous on stems and leaf bases, forming black lines where they break through the epidermis. It is the telial stage that gives this fungus the name *black stem rust*. Under the microscope the spores appear as dark brown two-celled structures. When first formed, each of these cells has two nuclei which soon fuse, making uninucleate cells.

For some reason, the black phase is much more injurious to the host than is the red phase, and plants which are so retarded that the teliospores develop before the maturity of the grain, produce almost nothing. Spring wheat is usually damaged much more than winter wheat because it matures later in the summer, after the rust has reached the telial phase.

The mature teliospores are sometimes carried considerable distances by the wind or they may remain attached to the straw for several months. They usually fall to the ground after a time, where they remain through the winter. No host is required for their germination, and they are entirely unable to infect wheat plants.

BASIDIAL PHASE. The next phase in the life cycle is a very inconspicuous one, but is significant in many ways. Early in the spring the teliospore germinates, each of the two cells undergoing meiosis and putting out a short piece of haploid hypha usually only four cells in length. There is some difference of opinion as to how much food this mycelium absorbs saprophytically from whatever organic material may be present, but it is certain that this phase is not dependent upon any living host. (See illustration on this page.)



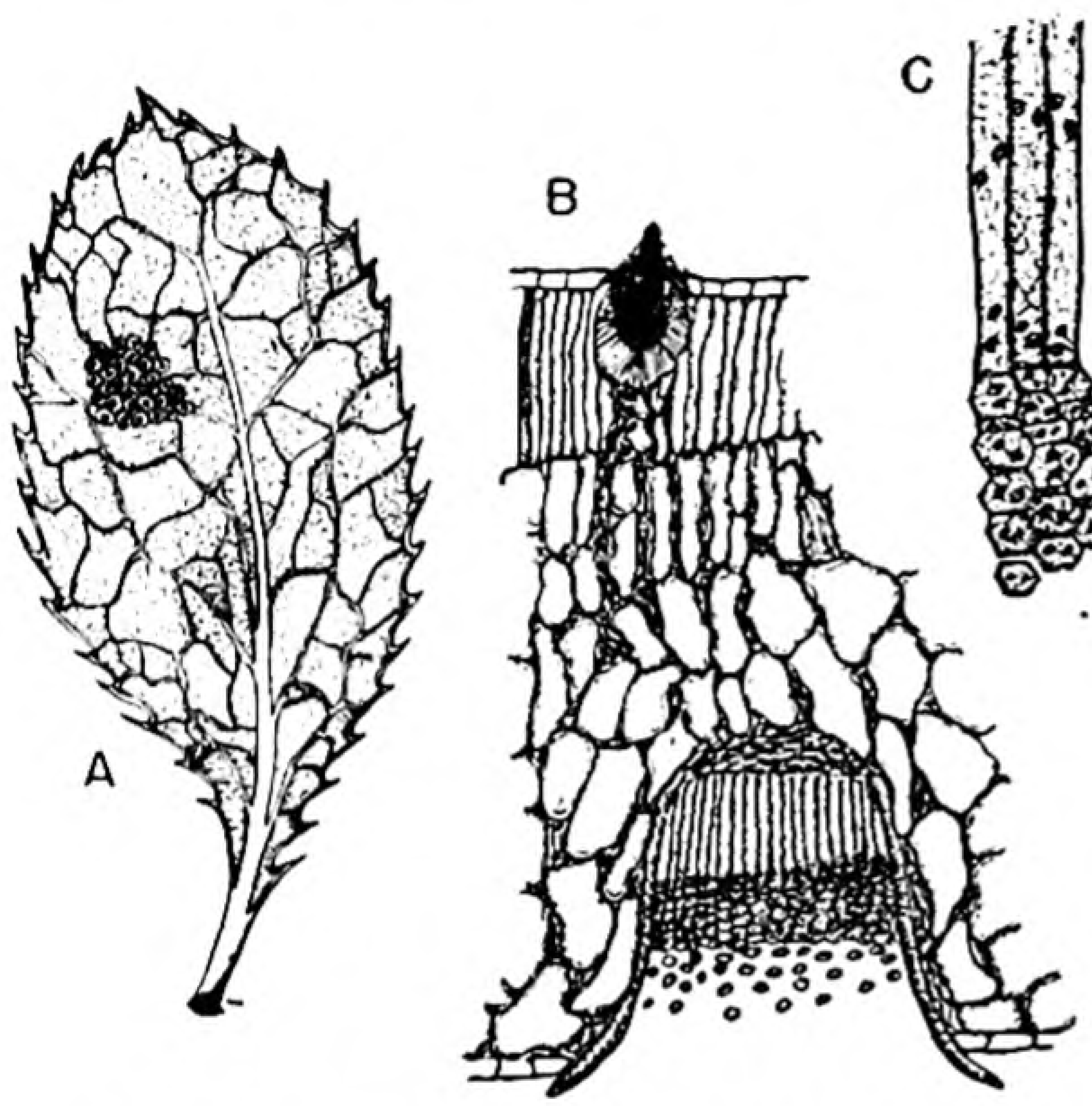
Telial and basidial stages of wheat rust.

Each cell of the hypha produces an external spore on a slender stalk. This four-celled structure seems to be equivalent to the four-nuclear basidium of the fleshy fungi. Hence the spores are *basidiospores*.

The basidiospores are so small that they are probably carried long distances by the wind. They can infect only a few species of plants, one of the most important of which is the common barberry (*Berberis vulgaris*).

SPERMATIAL PHASE. The basidiospores reach the barberry plant early in the spring when the leaves are young and tender, and infection is easily ac-

complished. As each spore germinates, the mycelium penetrates the leaf and spreads until a somewhat thickened, discolored spot is formed. In a short time there appear in the diseased area, usually on the upper side of the leaf, a number of small, elevated dots. In cross sections of the leaf, each of these proves to be a flask-shaped cavity (*spermogonium*), inside which very small uninucleate sporelike cells, the *spermatia*, are formed at the tips of delicate hyphae. The spermatia ooze out in a small drop of thick, sweet liquid. Other hyphae within the spermogonium develop in a different manner. Each one contains a nucleus at its base while the outer end extends far out, acting as a trichogyne.



Spermatial and aecial phases of wheat rust. (A) Barberry leaf with cluster of aecia. (B) Section through leaf showing spermatium in upper surface, aecium in lower part, and hyphae among host cells of mesophyll. (C) Binucleate aeciospores forming at ends of filaments.

For many years there has been much speculation, but no good evidence from observation or experiment, as to the function and significance of the spermatia. Recent work, however, shows conclusively that they are concerned in a peculiar type of sexual reproduction found only in the rusts.

Two kinds of basidiospore are now known to be produced. Although they and the mycelia that grow from them have the same appearance, they are clearly male and female; or, since they appear exactly alike, they are often designated + and −.

Under experimental conditions, when a diseased spot has been caused by infection with a single basidiospore and kept carefully isolated from others, no development occurs beyond the formation of a spermogonium. But, when a + spermatium is introduced to a − trichogyne; or, vice versa, the spermatium nucleus reaches the egg nucleus at the base of the trichogyne, much as would occur in a red alga. In the rust, however, nuclear fusion does not take place. Instead, a binucleate cell, (a *dicaryon*) organizes. A series of mitotic divisions in which both nuclei always take part gives rise to a dicaryotic hypha which grows between the leaf cells. A large number of such hyphae usually form. These, acting together, break through the tissues of the lower surface of the leaf, forming the *aecium*, which develops as a cup-shaped growth on the lower side of the leaf. In nature this transfer of spermatia is probably accomplished chiefly by insects which are attracted by the sweet liquid around the spermogonia.

AECIAL PHASE. The fully developed aecium is a cuplike structure set deep in the lower surface of the diseased spot and is filled with a large number of yellowish *aeciospores*. The numerous hyphae and the spores themselves are binucleate.

By a series of mitotic divisions alternate cells become aeciospores and the others, which are very small, soon disintegrate and disappear.

The aeciospores are scattered by the wind and if they fall on wheat plants or some other grasses which may serve as hosts, they germinate and the hyphae enter the tissues of the hosts through stomata and proceed to produce the uredinial phase, which is binucleate throughout.

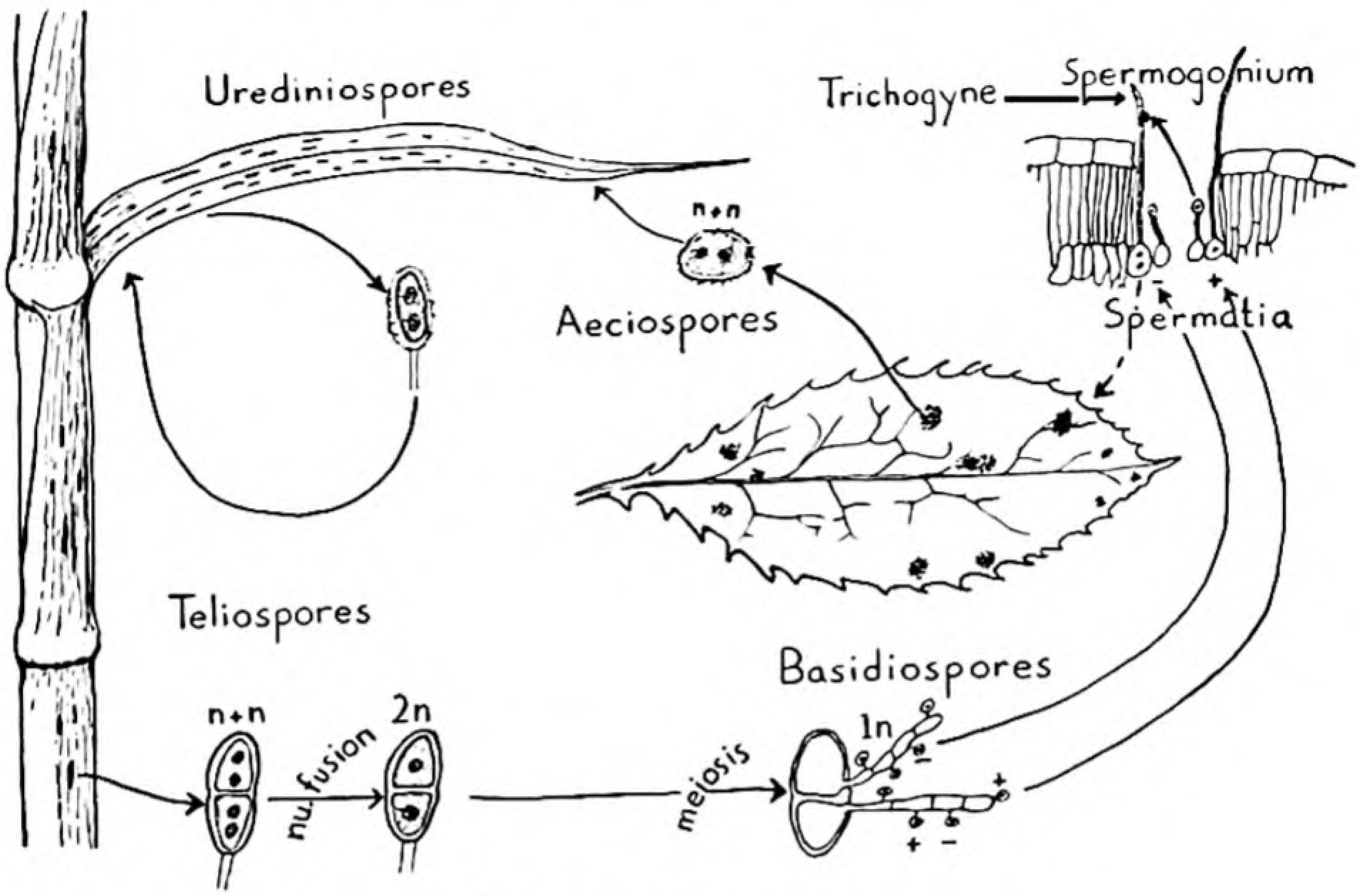
LIFE HISTORY IN THE RUSTS. In the discussion of the spermatial and aecial phases it has been suggested that there is a form of sexuality in the rusts, but there are some further facts that do not appear in an ordinary observation of the different phases because they involve nuclear changes which are visible only in specially prepared material. Reference to the diagram on p. 249 should clarify these points.

Each basidiospore has one haploid nucleus, as does every cell of the mycelium of the spermatial phase which follows. When sexual union takes place, initiating the aeciospore-producing hyphae, there is no fusion of nuclei as in ordinary fertilization, but each aeciospore contains two nuclei, presumably one from each parent mycelium.

When the aeciospore germinates and infects a wheat plant again, every cell of the mycelium of the uredinial phase has two nuclei, and this condition continues on through the telial phase and into the formation of the teliospore. Both cells of the young teliospore have two nuclei, but these soon fuse, so that the mature teliospore has a single diploid nucleus in each of its cells.

The reduction division occurs as the teliospore germinates, and all the cells of the mycelium of the basidial phase, as well as each basidiospore, is haploid. Sexual differentiation occurs here and two of the basidiospores produced by a basidium are female, and the other two male. The gametophyte generation then, begins with the basidium and continues to the initiation of the binucleate aecial stage. The sporophyte generation begins just before the formation of the aeciospores and continues through reduction division, which occurs during the germination of the teliospores.

The details of this complicated life history can be brought together into a sort of diagram which shows, in one picture, the relationships of the different phases. In studying this diagram a number of points should be carefully noted. No spore



Life cycle of wheat rust.

is involved as a connecting link between the uredinial and the telial stages. Instead, the same system of mycelium in the wheat plant simply changes over gradually from the production of urediniospores to that of teliospores. The uredinial phase can reproduce itself repeatedly if the proper host is available. This capacity is not known to occur at any other step. If living wheat plants were present throughout the year, and the climate were not too severe, it would seem that the rust might propagate itself indefinitely in the uredinial phase. Whether or not it actually does this in the great wheat-growing regions is a matter of controversy.

THE BARBERRY AND WHEAT RUST. That the barberry shrub was in some way concerned in the prevalence of wheat rust has been known for a long time. In at least one of the American colonies before the Revolution, a law was passed to regulate the planting of barberry in wheat-growing sections. In recent years, as the economic problems of agriculture have become more acute, there has been a renewed interest in the question.

Even if the complete extinction of barberry would not entirely eradicate the wheat rust fungus (since it may possibly winter over in the uredinial phase, especially in the warmer parts of the wheat belt), the effort yields worthwhile results in reducing the amount of damage done. The economic significance of a disease like this depends not so much upon its mere existence in an area as upon its prevalence and it is significant that the presence of infected barberry plants in a given wheat-growing district brings about a rapid spread of the infection. Mutations are frequent in the haploid basidial phase and hybrids occur freely on barberry. Therefore wheat rust becomes more versatile because the barberry acts as a breeding ground for new strains of the disease. By some such means as this, even rust-resistant wheat is frequently attacked.

A word should also be said about the barberry itself. The species that brings about the greatest amount of spread of the infection was apparently introduced into America from Europe in early colonial days and has spread westward with the movement of the population. It was planted as an ornamental and in some localities the berries had a limited use. On the whole, however, it is of so little value that its loss should cause little inconvenience. In many places it has become so well established that it propagates itself as a wild shrub in pasture lands and along roadsides and fences. In addition, in some parts of the country, especially in the West, there are several native species also that are susceptible to wheat rust. The European barberry (*Berberis vulgaris*) should not be confused with the much smaller Japanese barberry (*B. Thunbergii*) which is now extensively planted as a low hedge. The latter is entirely immune to wheat rust.

SOME OTHER RUSTS. There are thousands of species of rust fungi living as parasites on a great variety of vascular plants. Many of them alternate between two hosts, as does the black stem rust, while others require but one.

CEDAR-APPLE RUST. The cedar-apple rust (*Gymnosporangium Juniperi-virginianiae*) is another of those requiring two hosts. The telial phase lives on the common juniper (red cedar) tree, causing portions of the twigs and leaves to enlarge into brownish knots which are often mistaken for reproductive structures of the tree. These knots, commonly known as "cedar apples," form late in the summer and remain attached to the tree through the winter, the fungus living inside in the form of the telial mycelium intermingled with the tissues of the host. In the early spring, two-celled teliospores are formed, each on a long gelatinous stalk. After a warm rain, these stalks absorb water and swell in such a way that dangling orange-colored columns of teliospores are thrust out. They germinate immediately and produce basidiospores, which are scattered by the wind.

The basidiospores can infect only an apple tree or some closely related plant. Both cultivated apples and wild crabs are susceptible. The aecial phase on apple leaves, produced by the basidiospores, is much like the corresponding stage of wheat rust on barberry. The aeciospores mature late in the summer and are carried by the wind. Those which happen to become attached to a juniper tree may produce the telial phase again.

It will be noted that this rust has no uredinial phase. Consequently, both hosts are necessary for its continuation and it can be controlled by the eradication of either the apple or the juniper, the selection of the one to be sacrificed depending upon the relative value of the two in a given locality.

The Smuts. In many ways the smuts seem to be closely related to the rusts, there being numerous parallelisms between the two groups. Nevertheless, when contrasted with some of the rusts (Uredinales), the smuts (Ustilaginales) have a much less complicated life cycle.

The common name, smuts, arises because most of them produce masses of dark, almost soot-colored, spores (chlamydospores) that soil or smudge any object touching them.

Members of this group produce disease in hundreds of species of flowering plants, ranging from wild grasses and weeds to crop plants such as corn, barley, oats, wheat, rye, rice, the sorghums, millet, onion, and spinach. In some major crops damage is severe, causing serious financial losses to farmers. Corn smut is most destructive, reducing the corn crop of the United States an estimated average of 50 to 80 million bushels per year.

CORN SMUT. To understand this parasite and its life cycle it is necessary to have in mind the structure of the host plant as well as that of the fungus. Corn (*Zea mays*), in common with other grasses, has a delicate meristematic zone just above each

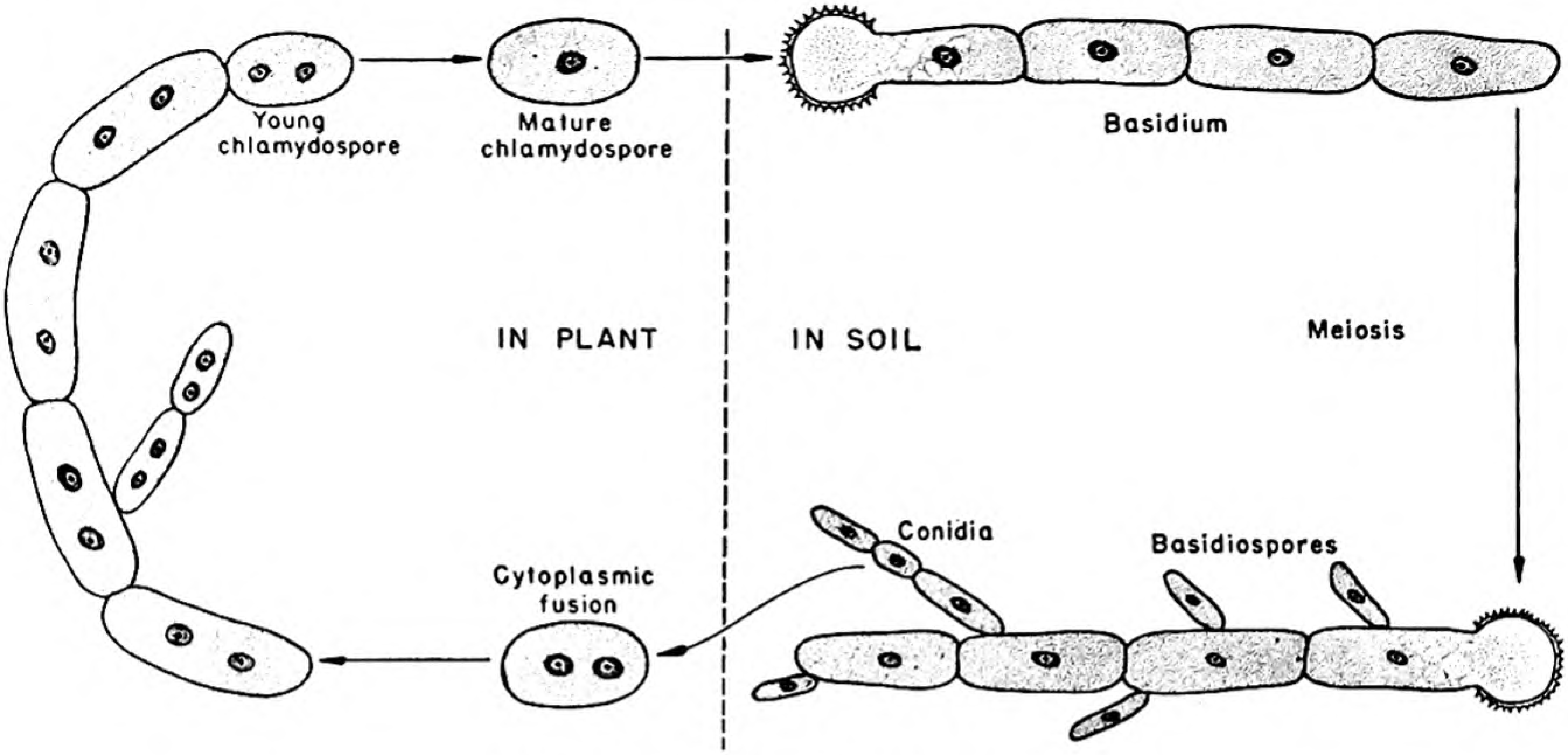
Ear of corn with smut boil due to *Ustilago zeae*.

node with its axillary bud (see p. 119). This region is encased by the leaf sheath (p. 26). These immature stem and bud structures, together with those of the developing tassel, are the parts of the entire plant most susceptible to smut infection. Basidiospores and conidia, to be discussed later, are carried by air, lodge in the leaf axil, and drift down the interior of the sheath. There they may germinate in contact with this "rudimentary ear," the meristematic axillary bud, or other rapidly growing structures they chance to touch. The hyphae penetrate the tissues and in from 6 to 14 days a characteristic smut gall may take form. At first the gall is covered by the highly polished epidermis of the corn plant, but soon it becomes dry and bursts open, permitting vast numbers of chlamydospores to become scattered in all directions. These usually overwinter in the soil, in fragments of decaying corn stalk or in stable manure. If the infected corn is used in ensilage, however, the spores soon die.

In the soil germination may occur under any conditions suitable for the growth of corn. Usually these occur the following summer when temperatures rise to the 80's or 90's. Chlamydospores may live as long as five to seven years without germinating.

Characteristically, the germinating chlamydospore gives rise to a four-celled basidium much like that produced by the teliospore of wheat rust. In corn smut, however, the basidiospores are somewhat elongated. They bud in a yeast-like manner, pinching off a series of conidia. Of the four basidiospores, two are of one sex and two of the opposite and the conidia produced by any given spore are of its sex. When basidiospores or conidia germinate, the resulting microscopic hyphae grow through the epidermis of the host where they continue to elongate. If two hyphae of opposite sexes come in contact with each other, conjugation takes place, producing a bi-nucleate cell or *dicaryon*. Repeated simultaneous nuclear divisions, accompanied by wall formation, maintain the binucleate condition in the rapidly growing mass of hypha. This hypha extends through the intercellular spaces of the parenchyma of the host plant and sends absorptive outgrowths or *haustoria* into some of the cells. In turn, these outgrowths divide and enlarge enormously and, together with the greatly enlarged fungal mycelium, become the massive gall. After a time the host cells die and collapse and the cells of the fungus become spherical, secreting thick walls. These bi-nucleate cells are the young chlamydospores. Soon, however, the nuclei fuse sexually and make a single diploid nucleus in each. These are the final steps in the development of the chlamydospores.

At about this stage the chlamydospores become scattered into the surface of the soil where they remain until hot weather stimulates them to germinate. During germination a rèduction division occurs and a four-celled basidium results which gives rise to the four sexually differentiated basidiospores. These basidiospores, or the conidia they produce, are the infective agents. Air currents scatter both basidiospores and conidia far and wide. Those that chance to fall into suitable places germinate, beginning the cycle all over again. The



Life cycle of corn smut, *Ustilago zeae*.

accompanying figure is a diagram summarizing this life cycle.

For many years serious attempts have been made to control corn smut in order to reduce the ravages on one of the world's great food-producing plants. Since the infective agents are strictly air-borne, only a limited number of points are open to attack on the disease. In small fields, it is sometimes feasible to destroy all the infected plants before the chlamydospores mature and become scattered, thus protecting the soil from this reservoir of infection. A more successful form of soil sanitation results from rotation in which crops other than corn are grown in a given field two years out of every three. In this way many of the spores die in the absence of a suitable host in the years when corn is not being grown.

Plant breeders are attempting to develop smut-resistant strains of corn, with little success thus far. At least one reason is that mutations in this fungus, as in others, continually produce new strains, some of which vary considerably from the parent stocks. Since there is a sexual step in the life cycle, hybridization occurs frequently, adding to the complexity of the situation. Both rust and smut resistance in host plants frequently comes to be of little avail when new, more virulent strains of the parasite arise. And so continues the race between the scientist and the farmer, on the one hand, and, on the other, the scores of strains of pathogenic fungi.

OTHER SMUTS. Corn smut is quite different from any of the others in appearance, but the stages in the life cycle of all are much alike. Because of certain peculiarities, however, control measures are possible in some of the smuts of small grains. A few of these will be discussed here.

BUNTS (*Tilletia*). Two of the bunts attack wheat causing extremely heavy losses. These are *T. tritici* and *T. levis*. A third, *T. horrida*, is a serious parasite on rice. Bunt in wheat is often called covered smut because the chlamydospores tend to remain where they are formed within the blackened and slightly distorted grain. This structure is referred to as a bunt ball. Another common name for this disease is stinking smut, appropriate because crushed bunt balls have the unpleasant odor of decaying fish. The odor is due to trimethylamine and it may impregnate the whole threshed crop if the disease is widespread in the field. When the spores are dry at threshing time, they may also cause other economic losses by giving rise to dust explosions, wrecking threshing machinery.

During threshing or other handling of infected wheat, bunt balls (diseased kernels) are broken

open and the chlamydospores become scattered over the surface of uninfected wheat grains, adhering to them. When such wheat begins to grow after planting, conditions are often suitable for germination of these chlamydospores, and the resulting hyphae penetrate the young wheat plant. In contrast to the localized infections of corn smut, bunt fungal hyphae extend throughout the entire wheat plant. Chlamydospores, however, are predominantly formed only in individual grains of the head of wheat (also of oats, sorghum, and rice) to form the bunt balls.

An examination of this life cycle shows clearly that the vulnerable point for control lies in the seed-borne chlamydospores. For this reason, seed is sterilized by various means that do not reduce the viability of the wheat. The more modern sterilizing agents are applied in the form of dusts mixed with the grain before it is planted. Such treatment plays a large part in reducing or almost eliminating losses from bunt. In parts of the country where the chlamydospores remain alive in the soil and seed treatment is ineffective, bunt-resistant strains of wheat are being grown with complete success.

Loose Smut of Wheat (*Ustilago tritici*). This type of smut is distinguished from covered smut, or bunt, by the fact that the chlamydospores, having fallen away and left the rachis almost bare, are soon set free.

The fungus overwinters, not in the form of spores but as mycelium, inside grains that seem to be normal. When such wheat germinates, the mycelium grows into every part of the seedling and produces masses of chlamydospores throughout the head. These spores are wind-borne, becoming attached in a pollen-like manner, to stigmas of normal wheat flowers. By-passing the basidiospore stage, the chlamydospores infect the developing embryo directly, but without destroying it. When this wheat grows the following year, the fungus develops with the seedling, and prevents the formation of its grain. Since external treatments cannot reach the fungus within infected wheat grains, there is no successful method of control other than heat. By skillful application of high temperatures it is possible to kill the fungus without devitalizing the wheat embryo.

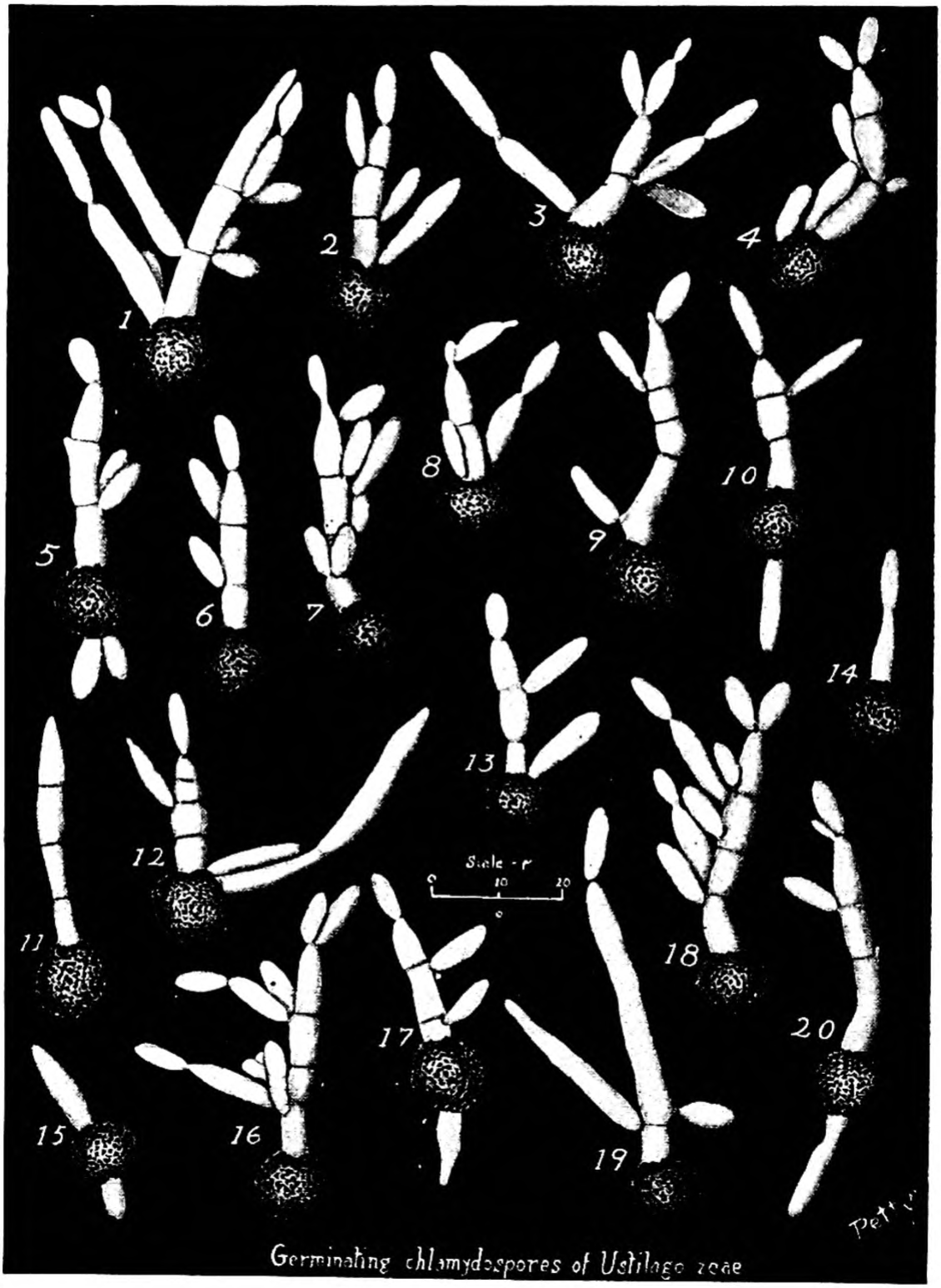
The preceding discussion of a few representative smuts illustrates the following fact that, botanically speaking, smuts are an interesting group of plants. From the standpoint of the world's food supply, they are of the greatest negative economic importance. And, finally, successful control of such pathogenic organisms depends, first of all, upon a thorough knowledge of the entire life cycle of both host and parasite.

Altogether smuts comprise approximately 600 species of fungi pathogenic to other plants. In all, the chlamydospores are thick walled and either black or brown. They germinate to produce intercellular mycelia in most host plants whose cells are penetrated by haustoria and, in this manner, extract nourishment. Abnormal growths on the host plant are rare; however, in corn, the grains frequently become greatly enlarged and distorted.

Origins of Fungi. The different groups of fungi are almost certainly degenerate strains from various algal groups. That their ancestors must have had chlorophyll seems almost axiomatic. No source is known other than chlorophyll-bearing plants from which the early fungi either could have derived their food or could have inherited their forms. All present-day species must have organic food from outside sources if they are to survive, and there is no reason to suppose that their early ancestors were different from them in this respect.

The loss of ability to produce chlorophyll is very common in all groups of plants. In fact, a single gene mutation is often sufficient to bring about this change. It is true that the majority of common plants are unable to absorb food from outside sources, and that they starve to death whenever they are unable to carry on photosynthesis. On the other hand, there are a few of the Chrysophyta and the Volvocales and their near relatives that are able to carry on photosynthesis whenever conditions are suitable and to absorb organic food in an animallike fashion whenever it is available. Some of the obvious relatives of these plants are devoid of chlorophyll, always leading the lives of primitive animals or of fungi.

Comparison of the Myxomycetae with some of the rarer orders of golden algae strongly suggest



Germinating chlamydospores of Ustilago zeae

close relationships between them. In fact, many biologists are inclined to believe that some of the primitive animals and the slime molds may have arisen from the Chrysophyta or, more probably, from their ancient ancestors.

A few of the Phycomycetae seem to be closely related to the coenocytic green algae, but the majority appear to have evolved too far to permit the recognition of their parental stocks. Nevertheless, evidences of a green-algal ancestry of these coenocytic fungi are rather strong.

A considerable number of the Ascomycetae and Basidiomycetae have a trichogynelike structure as a part of the female sexual apparatus. Both the trichogyne and the behavior of the nuclei, as well as methods of spore formation, are sufficiently similar in the two groups to cause many botanists to suppose that the sac fungi have been derived from the ancient red algae.

The basidiomycetes are so very much like ascomycetes in many ways that they are usually considered to be descended from a common ancestor. In fact, the most obvious distinction between these two groups is the production of spores inside a special cell wall in the case of the ascomycetes, and outside on stalklike sterigmata in that of the basidiomycetes.

Parasites and Scavengers. Since the various fungi do not have chlorophyll, their ultimate sources of food must all be outside themselves if they are to survive. Some species have evolved mutual relationships with other plants, but the majority have developed means of living saprophytically, parasitically, or both. Saprophytes reduce nonliving organic materials to simpler forms which they absorb, using the stored energy and nutrient materials in their own metabolism. The parasite on the other hand, when growing within the tissues of another organism, more or less completely deranges the structures and metabolic activities of living protoplasm. Such disturbance is commonly called *disease*.

Different parasitic fungi have widely different effects upon their hosts. Some penetrate the tissues so little and take such a small amount of food that their effects are almost negligible; some retard the growth of the entire plant, or of its organs, resulting in a stunted development; others kill a part or all of the tissues outright; and still others stimulate certain parts of the host to abnormal overgrowth, producing galls or other abnormalities. In many instances the fungus obstructs the vascular tissues, and the result is a wilt disease such as that of cucumbers and melons. In addition to these, there is a great array of parasitic or semiparasitic organisms which cause the decay of grains at harvest time and of seeds in the soil, and of those that are responsible for the many types of fruit and vegetable rots.

These various effects produced by fungi upon living organisms are only partly due to the food which they absorb or to the mechanical injury caused by their presence. Probably a much more important, if less tangible, source of damage is their production of substances, as by-products of their activities, that actually poison the protoplasm of their hosts.

Disease is often considered to be an unmixed misfortune to any organism so afflicted. Nevertheless, many more individuals in almost every species come into existence than can possibly survive. For this reason large numbers of plants and animals fail to have sufficient amounts of food to maintain life or vigor. Actual starvation probably causes some deaths among these organisms but in a fairly high percentage of cases bacterial or fungus diseases destroy the less vigorous ones, returning their substance to the soil and air, where it again becomes available for use by other plants.

Whatever the cause of death, the saprophytic fungi, in conjunction with bacteria, complete the process involved in breaking down the highly organized substances of protoplasm and walls of all available dead organisms, and the dead parts of living ones. Such processes of decay are actually the digestive and other metabolic activities of these scavengers of the plant world. Without such destructive processes the cycles of energy and nutrient materials discussed in Chapter 5 could not continue, and life as we know it would disappear from the earth because essential elements would be held permanently in complicated compounds that could not be utilized over again by green plants.

Clear examples of the work of saprophytes can be found in even a brief examination of almost

any forest floor. One has only to examine the scores of decaying twigs, stumps, or logs and the small valleys filled with moldering piles of drifted leaves and other detritus. Because of this kind of activity through the centuries the forest soils are often extremely fertile. The fungus scavengers return to the soil those minerals that have been combined in protoplasm and cell walls, and to the air the great supplies of carbon dioxide that can be used again in photosynthesis by the green plants that are still alive.

These fungi can grow in wood that man values as readily as in dead stumps in remote forests. In other words, any wood that is exposed to the weather or is subjected to constant moisture may be destroyed by fungal action. Therefore, almost any kind of wood that is used in the ground, such as fence posts, telephone poles, and railroad ties, needs to be given special treatment to protect it against the fungi of decay. Various methods are used but most of them include impregnation with creosote or some other fungicide. A few kinds of wood are highly resistant to decay because of substances that are commonly found in them. For this reason fence posts of osage orange, black locust, and red cedar are famous for their lasting qualities.

Certain species of fungi attack wood while it is still living, acting as parasites. In some cases these fungi cause serious damage to forest trees. Certain parasites bring about the death of the cells of the tree and then change their metabolic activities sufficiently to become entirely saprophytic, causing decay.

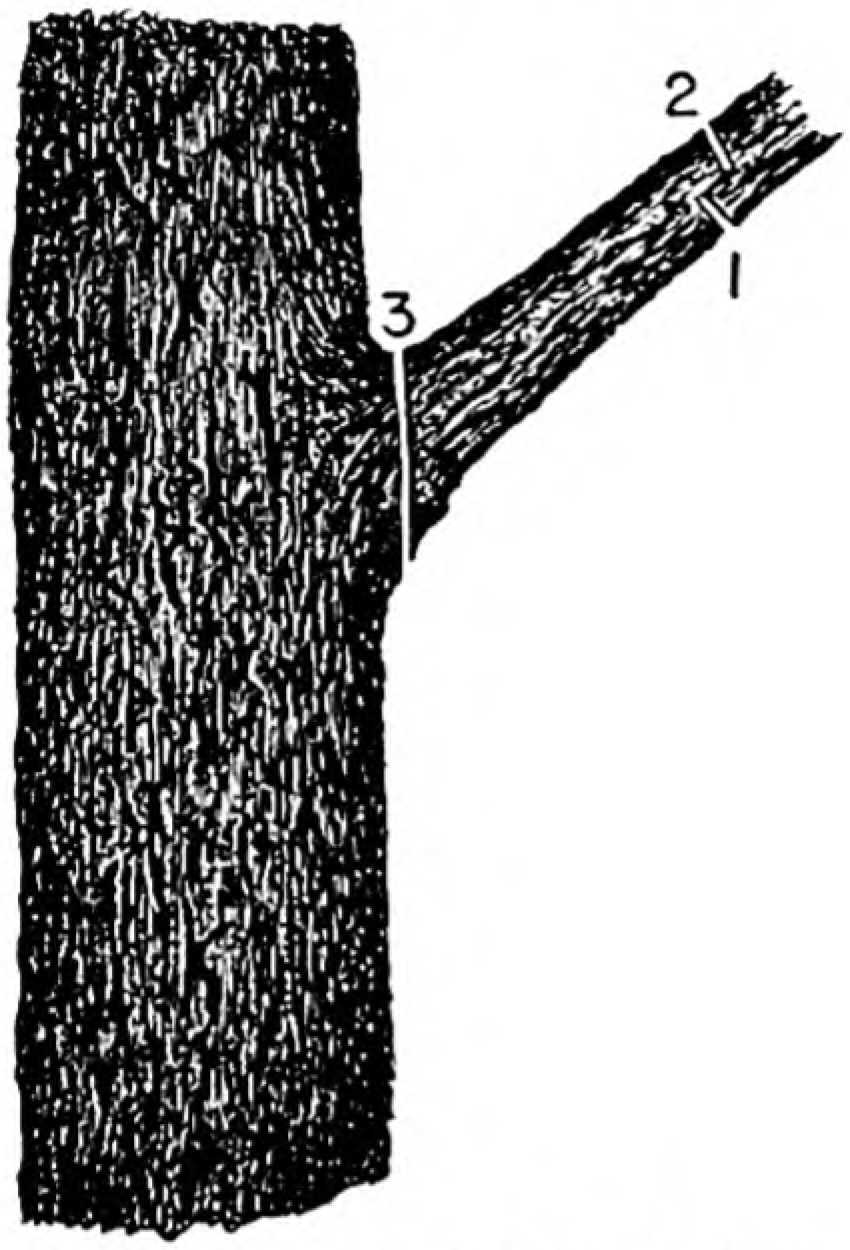
Under natural conditions in a native wild forest the total effect of these various kinds of fungi tends to strike a balance. The diseases largely eliminate the old or broken trees, leaving room for younger, more vigorous ones. But where forestry is practiced and wood becomes a cultivated crop, the parasitic fungi are often extremely difficult to control. In fact, along with wood-destroying insects and fire,

Results of very bad method of removing large branch at base of tree trunk, showing damaged bark below cut, with callus closing too slowly over rough, dead wood that is almost certainly infected.

Various stages of healing scars by means of callus where branches have been removed correctly.

they create some of the most serious problems of the scientific forester.

A somewhat similar problem confronts the person with a few shade trees planted about the home grounds. Here, the chief value does not come from



Steps in removing large branch from tree. Numbers indicate the order to be followed.

wood products but from the beauty and comfort lent by properly placed, well-formed green trees and the shade they cast. Under these conditions every tree and almost every branch has its own peculiar importance, and occasional pruning is necessary to maintain correct form and to control size.

Very often pruning brings about the introduction of fungus spores to the freshly cut or broken tissues. As examples, the unskilled worker may cut large branches in such a way that their weight causes them to split down the side of the tree trunk, opening areas of rough, irregular, but moist and living wood. Such surfaces are almost perfect places for the lodgment of spores and the propagation of mycelia. The resulting infections may give rise to a slow destruction of the interior parts of the tree, with its ultimate death or serious disfigurement. In addition, such scarred woody surfaces heal very badly. The reason is that healing must all result from the activities of the cut edges of the cambium, which normally forms a thickened enlargement called the *callus* at the margin of the wound. As time goes on the entire cut surface should become covered with new tissues which gradually close over the open space.

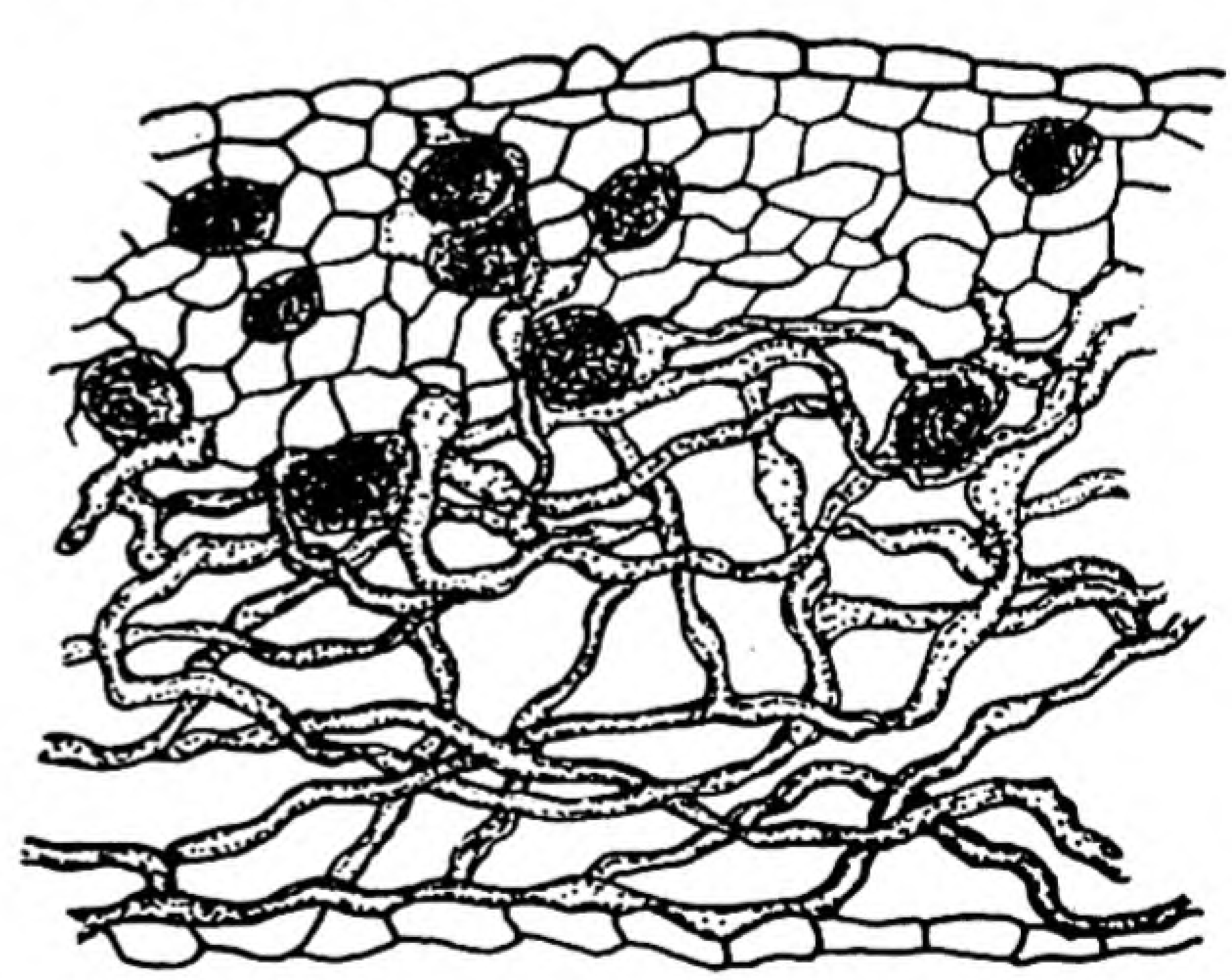
The following brief outline states the most important points to be observed in removing large branches from trees:

First, a cut should be made far enough from the tree trunk to prevent peeling of the bark. A succesful method is to notch the under side of the limb a foot or two farther out, then to saw it off. When it has fallen it is easy to make a smooth, clean cut with the saw close to the body of the tree.

Second, the wound should be sterilized and sealed. This can be done effectively by coating it thoroughly with ordinary house paint. This treatment brings about the destruction of spores and at the same time closes the cut ends of the water tubes, in this way keeping the wound sterile during the months or years required for healing to be completed.

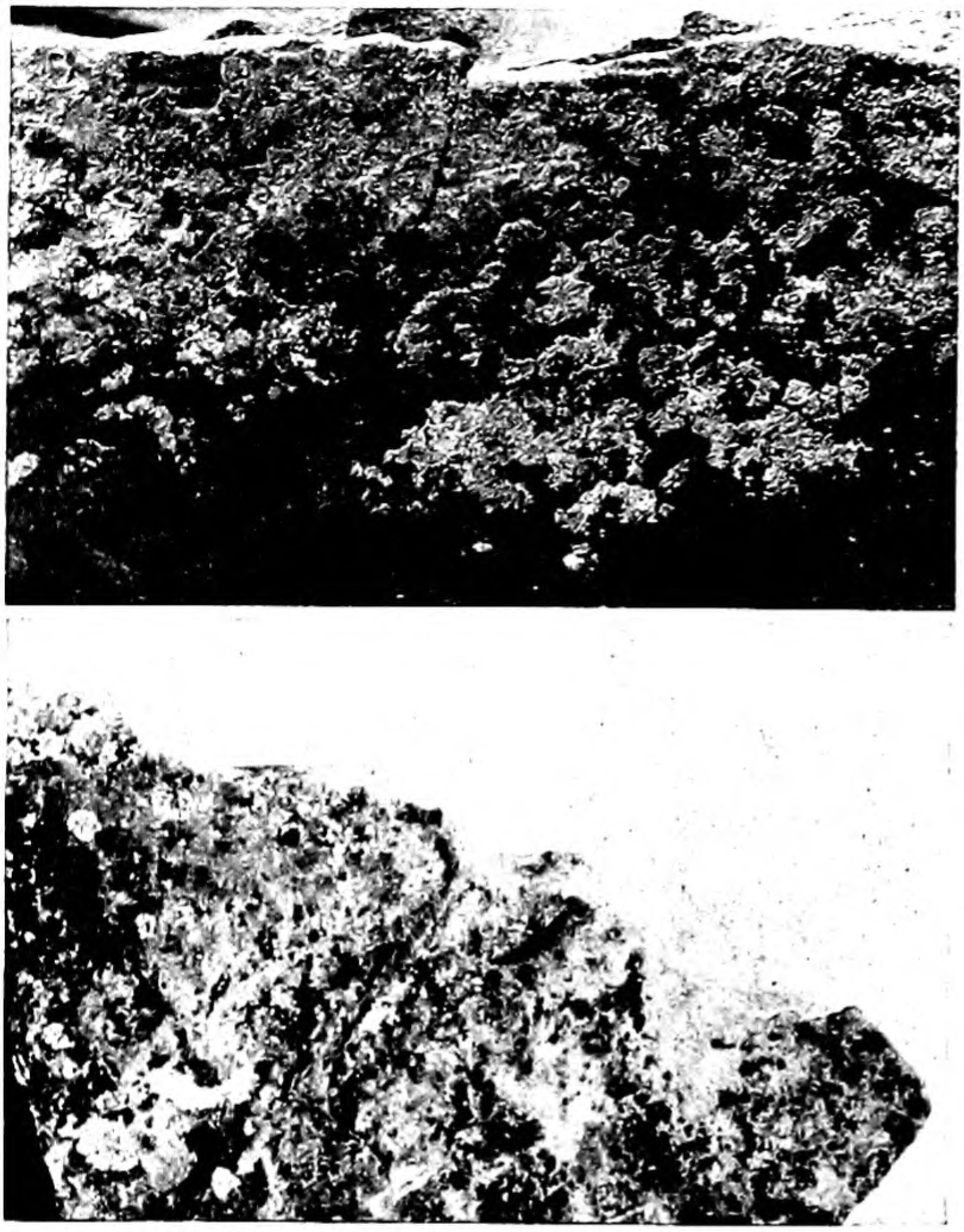
LICHENS

Lichens are to be found from polar regions to equator, yet they attract so little attention that few



Structure of lichen, showing dark algal cells surrounded by fungal hyphae.

persons recognize their presence. They take many forms and display numerous colors. Some of them have the appearance of irregular gray, black, yellow, or brown patches of paint on rock surfaces, on the bark of trees, or occasionally on the soil; others



Crustose lichens. Several species growing on rocks.

suggest curled, wrinkled, greenish-gray leaves, while still others are divided into finely branched threads or wider ribbons that hang from the twigs and bark of trees or that stand upright on the soil.

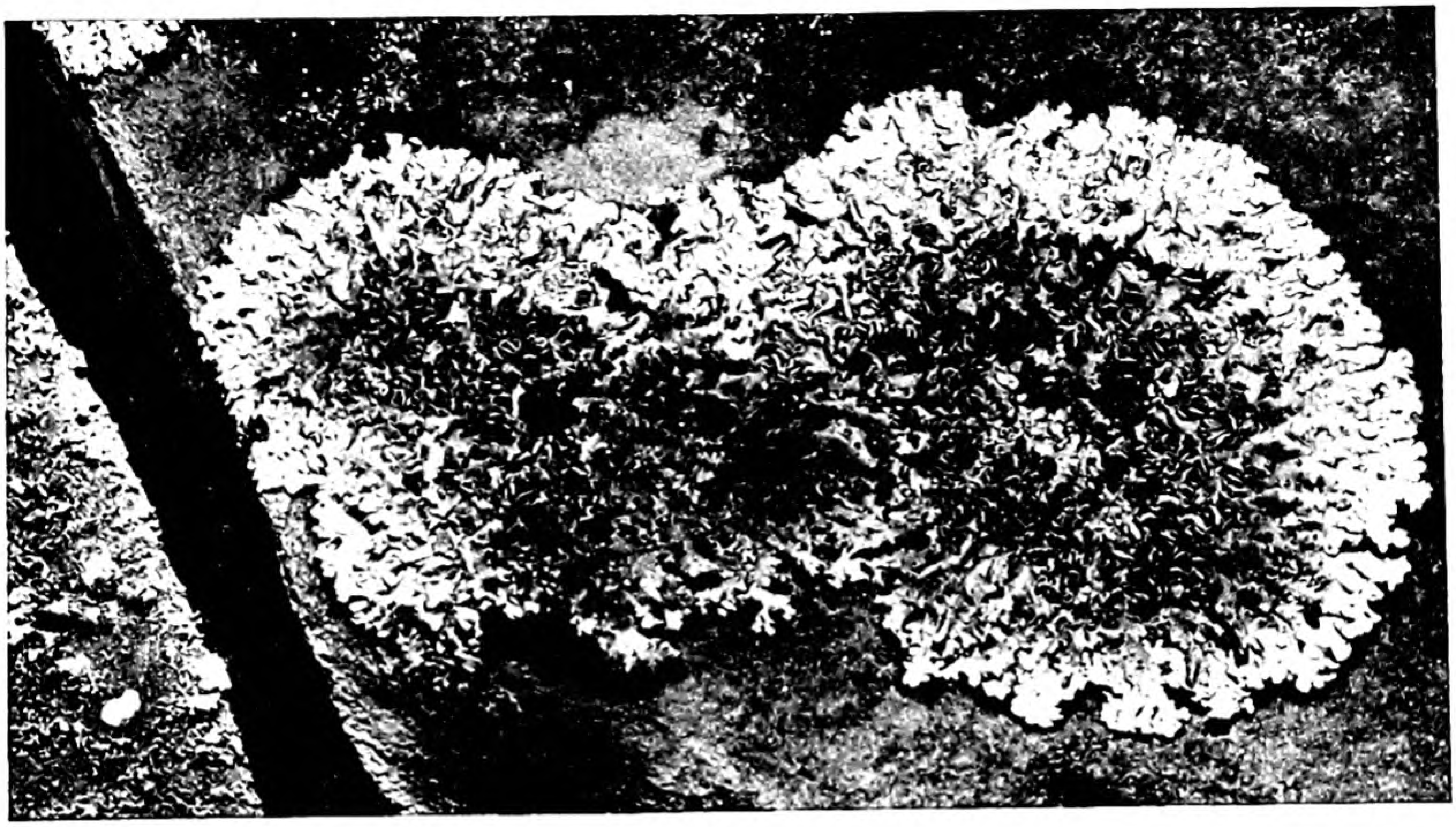
This group of plants occupies a peculiar biologic position. An individual lichen is, in fact, a combination of an alga and a fungus so intimately associated that they seem to make up a single plant body. The algae entering into the constitution of most lichens are either Cyanophyceae or Protochlorophyta. Such well-known genera as *Protococcus*, *Gloeocopsa*, *Nostoc*, and *Rivularia* are frequently met. The fungus is an ascomycete in all but a few tropical species, in which it is a basidiomycete. The lichen-forming algae are quite or almost identical with the free-living species that grow on tree trunks, in the surface of the soil, and in other similar places. The fungi are distinct from those that do not form lichens. The shape of the lichen is determined much more by the fungus than by the alga, the plant body being really a fungal mycelium with algal cells imbedded in it.

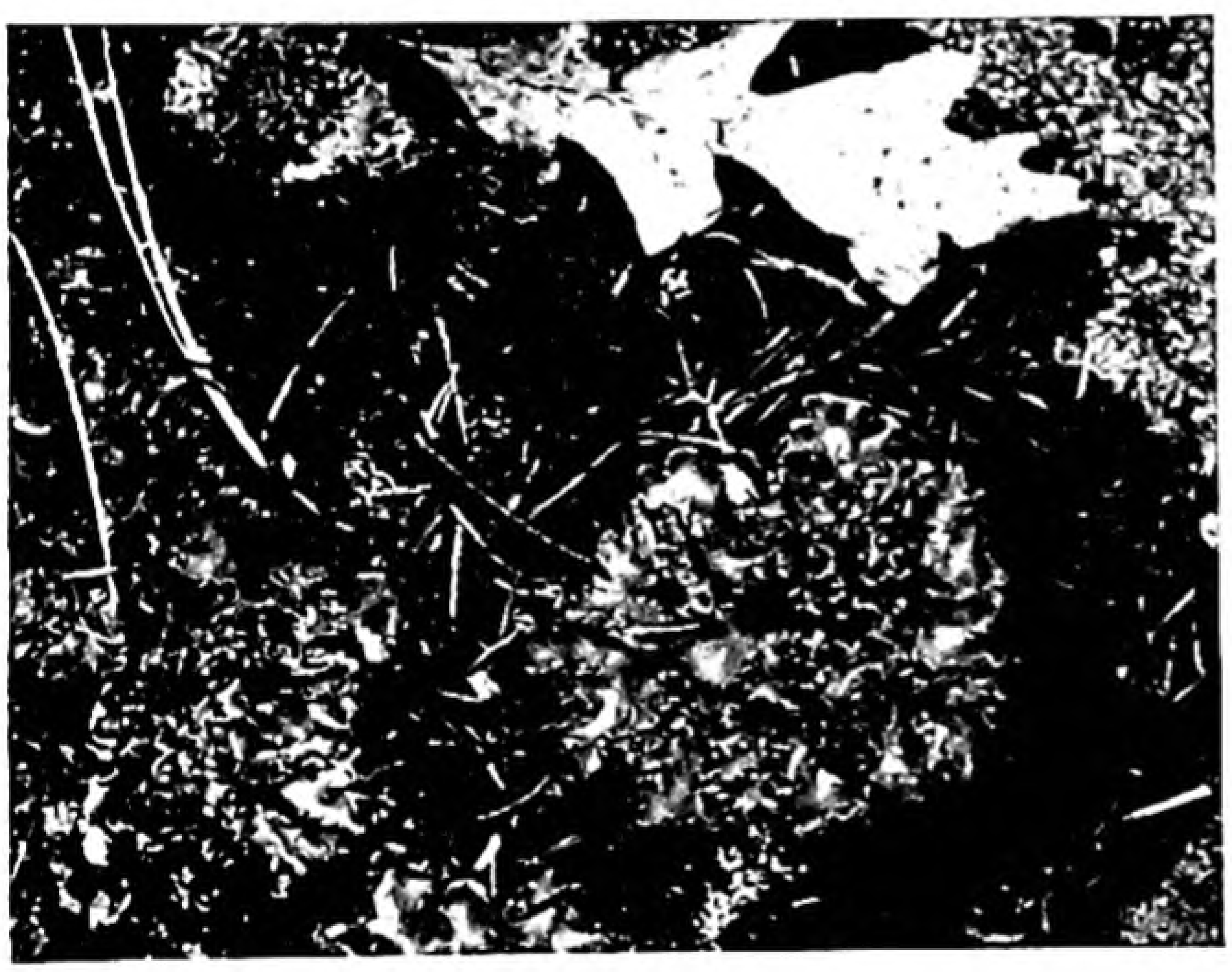
Classification. Logically, lichens should not be classified as such at all. Natural classification is based upon knowledge of evolutionary relationships and, since the two plants that form a lichen have had different origins, the alga might be placed with the other algae and the fungus with its nearest relatives. But each combination of a species of alga with that of a lichen-forming fungus produces a set of characteristics as definite as those of an ordinary plant. For this reason the lichens are treated as if they were not combinations but individual plants, and binomial nomenclature has been applied to them. Also, practical though very faulty artificial classification is widely used. In this system lichens are arranged in three groups, *crustose*, *foliose*, and *fruticose*.

Crustose lichens grow in the form of crusts firmly attached throughout to the substratum. In some species they are partly imbedded in rocks or other hard surfaces. Some of these are so inconspicuous that their presence is revealed only by the fruits, which appear on the surface of the rock.

The foliose forms are flat and rather leaflike. They are attached by only a limited area or at least their margins are free. All the bushy, finely branched forms are included in the fruticose group. Two of the best known genera are *Cladonia*, whose many species grow upright and include the "reindeer moss" of the Arctic, and *Usnea*, a form which usually hangs from the branches of trees.

Reproduction. Many lichens propagate extensively by simply growing and branching, the death of the older parts ultimately leaving the tips of branches as separate individuals. In many





Foliose lichens. (*Top*) *Parmelia* growing over crustose forms. (*Bottom*) *Peltigera* on soil.

species, however, special reproductive structures, known as *soredia*, separate from the plant body and form a dusty or mealy covering over the surface. Each soredium consists of one or more algal cells bound together into a compact mass by a few filaments of the fungus. The soredia have the same resistance to cold and desiccation that is characteristic of lichens in general and may be carried long distances before developing into new individuals.

In the lichens whose fungus is an ascomycete, which means almost all of them, an ascocarp also may be formed. This assumes different shapes in the various species but in all of them it has a specialized region in which the asci are developed. So far as is known, these fruits result from a sexual union of filaments similar to that in the cup fungi. Although the algal cells may be imbedded in the vegetative tissues of the fruit, they are not otherwise concerned in this reproductive process. The ascospores, which are often two-celled, reproduce the fungus only, and the mycelium developing from them must immediately make contact with the proper species of alga if it is to live. The fungi

Fruticose lichens. (*Left*) *Usnea*. (*Top, right*) Two genera growing together on branch of tree. (*Bottom, right*) *Cladonia* on soil.

of the basidiolichens also produce fruits in which basidia and basidiospores are borne.

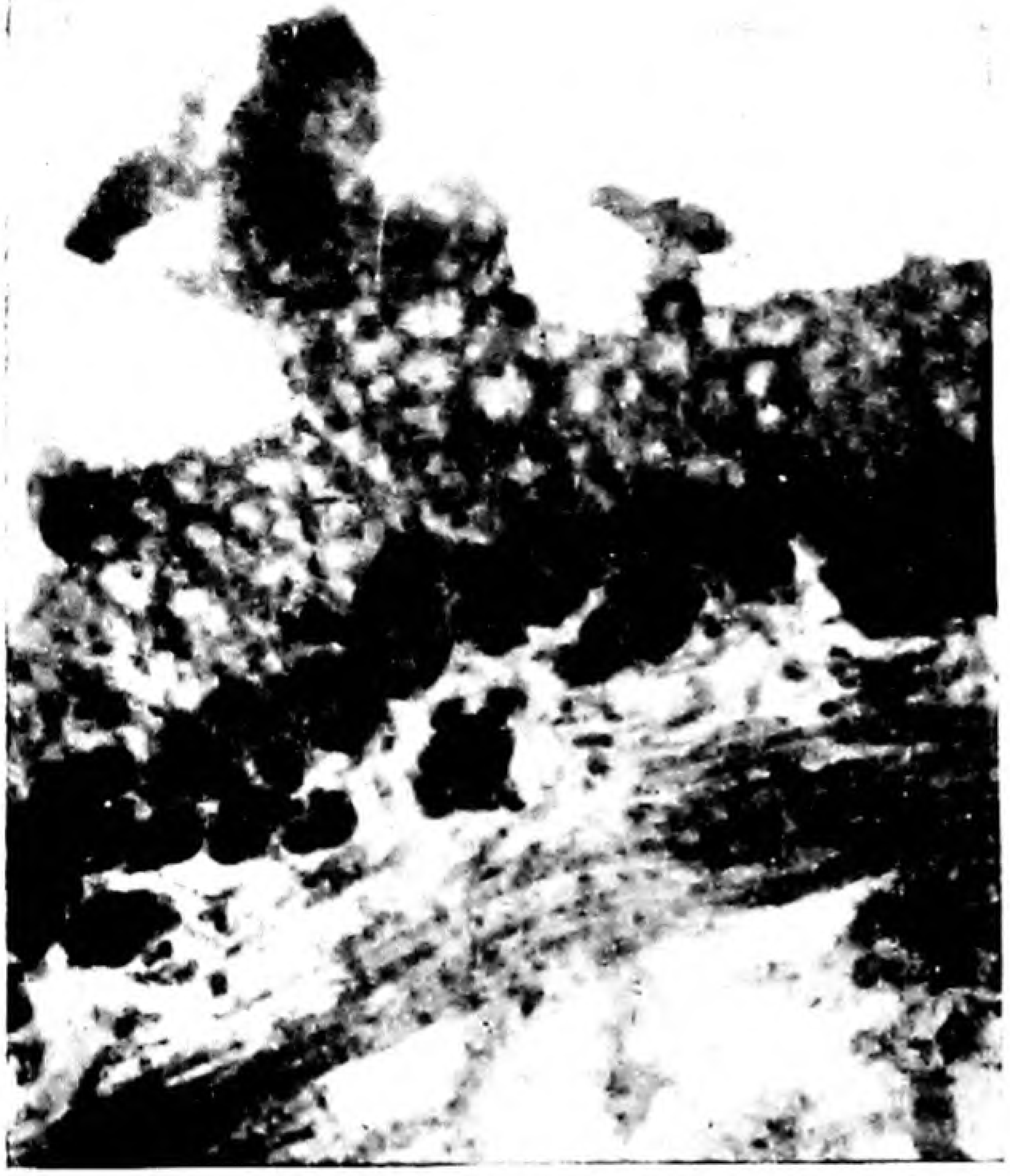
The Role of Lichens in the World of Life. Most lichens are extremely resistant to adverse conditions of moisture and temperature and can, therefore, grow in climate of any kind which supports life. In tropical forests they are abundant on trees, even to their leaves; they are a very characteristic part of the flora of rocky deserts; and they extend into the farthest outposts of plant life in arctic regions.

The crustose forms are the world's great pioneers. No organism other than a crustose lichen can maintain itself on a perfectly plain, clean rock surface. These plants are, therefore, of exceptional significance as forerunners of other kinds of life in rocky places.

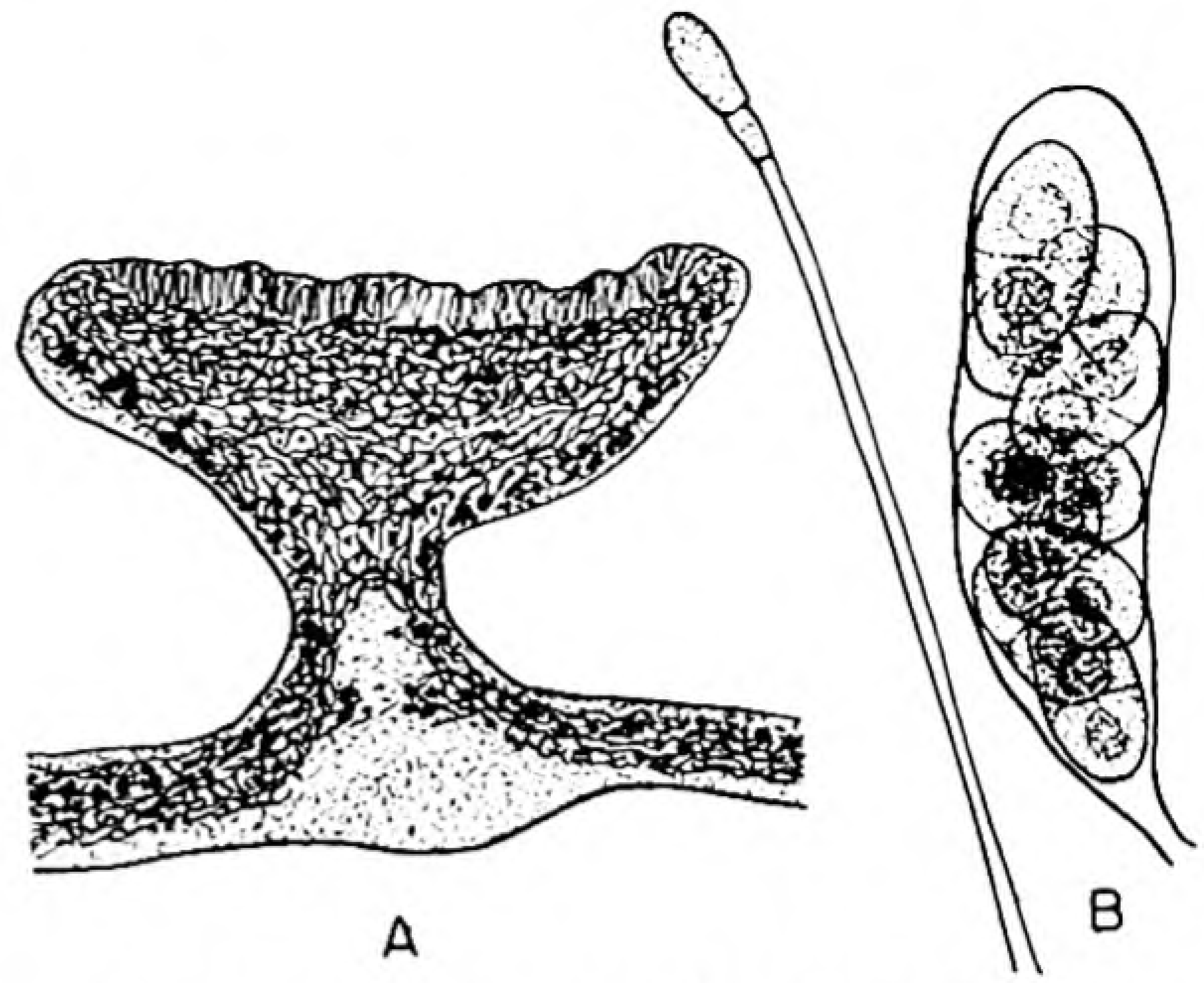
The establishment and growth of a crustose lichen on a bare rock is a marvelous phenomenon. A small tangle of fungus with a few algal cells becomes attached to the hard surface, but increase in size cannot take place until sufficient moisture comes, to permit the alga to carry on photosynthesis. Even then the fungus absorbs a considerable portion of the carbohydrate and enlargement takes place slowly.

At times, the tissues may be so dry that they could be easily ground to dust between the fingers. A shower or heavy dew permits the resumption of food synthesis and once again a little growth occurs. Thus, year after year, these hardy pioneers extend their domains almost immeasurably slowly.

During the long period of development of a crustose lichen on a rock surface the mycelia of the fungus often pry into crevices, gradually breaking loose small particles. In some cases secretions from the cells of the plant dissolve parts of the stone. In addition, dust often lodges on the surface of the lichen and with the death of its older parts minute bits of humus are formed. The mixture of sand, dust, and humus may become a trace of loamlike soil in which other small plants can live. Most often



Soredia. Section of lichen with soredia ready to break loose from upper surface. Note also, dark patches of algal cells and threadlike hyphae of fungus.



Ascocarp of lichen. (A) Section through elevated ascocarp showing asci and paraphyses on upper surface. (B) Ascus and paraphysis. Greatly magnified.

these are some of the hardier mosses. With their growth and death still more soil becomes organized and larger plants may take root in it. Without the pioneering activities of crustose lichens other plants could become established slightly or not at all in many places.

MYCORRHIZAS

Intimate associations between fungi and other plants of many kinds are very common. Sometimes

Close up photographs of ascocarps. (*Left*) On *Parmelia*. (*Right*) On *Usnea*.

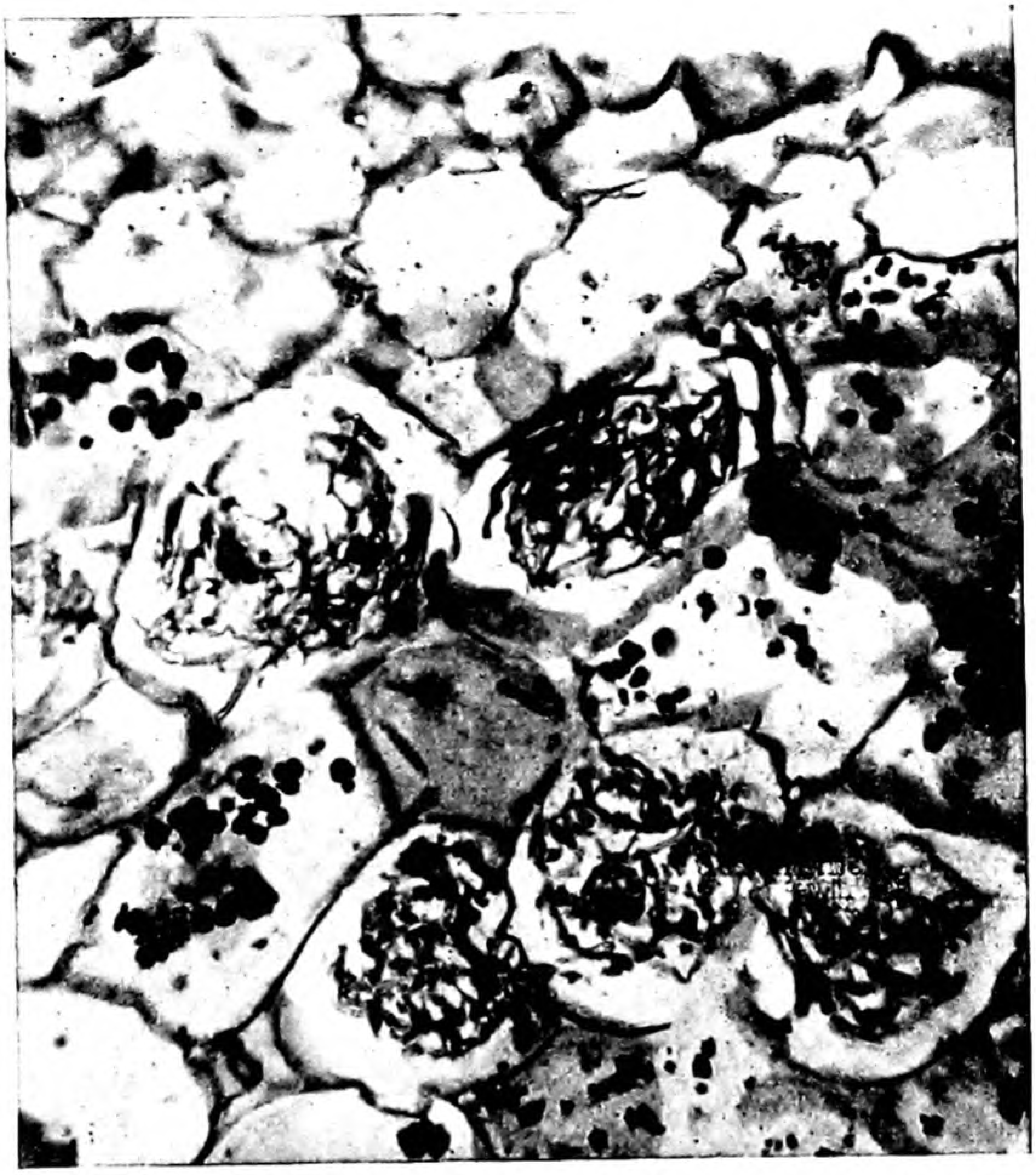
Ectotrophic mycorrhiza of pine tree as seen in cross section, showing fungal hyphae crowded in between cells of cortex of root.

the fungus merely acts as a parasite, absorbing food and in no way promoting the welfare of its host. The various plant diseases, such as the rusts, smuts, and mildews are of this type. On the other hand, in the lichens, the presence of the fungus contributes something to its green associate, making it possible for the two species, acting together, to live in places where neither could perpetuate itself alone.

A still different kind of association, rather similar to that of the lichens, occurs between certain soil fungi and the roots of many kinds of plants. These root-fungus combinations are called mycorrhizas (*mykes*, fungus; *rhiza*, root). Many of the forest trees have mycorrhizas in which the fungi are simply the mycelia of the mushrooms of the forest floor. The hyphae penetrate the outer layers of young roots, not by destroying the cortical cells but by growing between them. In this way a false cortex is formed, made up of a close association of hyphae and the outer layers of the root. Apparently the fungus absorbs some food from the green plant, thus receiving benefit. At the same time it digests and absorbs some of the humus of the soil. In turn the roots take a part of these nutrients from the fungus, in this way receiving value from the association.

The type just described goes by the name of *ectotrophic mycorrhiza* (*ektos*, outside; *trophikos*, nursing), referring to the fact that the fungus receives food from the green plant without actually entering its cells. A less frequent type is the *endotrophic mycorrhiza* (*endon*, within) in which the fungal hyphae grow from the soil into the living outer cells of the root. Such behavior reminds one of a highly advanced form of parasitism, and it would certainly be called by that name were it not for the fact that numerous green plants, such as many of the orchids, the cranberries, and a considerable number of others, not only have endotrophic mycorrhizas but are unable to thrive without them.

In some way as yet not fully understood, these fungi contribute substances that are essential to the



Endotrophic mycorrhiza of orchid as seen in cross section, showing hyphae within cells of cortex.

welfare of the green plant in whose roots they grow. In certain cases it seems that the fungus makes available needed nitrogenous compounds.

In some species of orchids even the seeds fail to germinate in nature without the presence of an appropriate fungus. In the laboratory, however, it has been found that certain sugars can be substituted, permitting the seedlings to develop normally. This discovery strongly suggests that the importance of the fungus to the embryo in the seed lies in the production of the proper sugar to permit growth of the orchid.

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Chapter 17

BRYOPHYTA: MOSSES AND LIVERWORTS

The chapter on fungi interrupted the narrative that shows the sequence of steps in the development of higher plants from the Protochlorophyta. With the Bryophyta the thread of relationship is picked up once again. The same chlorophyll-carotinoid complex, the terminally biflagellate sperms, and other anatomic and physiologic similarities as occur in certain classes of the green algae are carried on into the mosses and liverworts. But in the bryophytes both the sex organs and sporophytes are more complicated than are the corresponding single-celled structures in any of the Protochlorophyta.

The following three groups represent the most important bryophytes:

- The True Mosses
- The Bog Mosses
- The Liverworts
  - A Leafy Liverwort
  - Thallose Liverworts

Few people who are not botanists ever notice liverworts even to the extent of wondering what they are, and the name, moss, is often incorrectly applied to many plants that are not closely related to this group. In fact, almost any kind of small, green or greenish plant that seems superficially to be finely divided, branched, and tangled is likely to be called a moss. As examples, floating algae are incorrectly called by this name; reindeer lichens are called "reindeer moss"; old man's beard, a pendulous fruticose lichen, is sometimes called "tree moss"; and Spanish moss of the Gulf States is a seed plant far removed in relationship from all the others. In the botanical sense the use of the word, moss, is limited to the class known as the Musci. The Hepaticae constitute the remaining class of the Bryophyta, and are commonly called liverworts.

The *Bryophyta* (*bryon*, moss; *phyton*, plant) occupy the position among green plants next higher in the scale of complexity than the Protochlorophyta. They are distinguished from that division not so much by size or the degree of organization of the vegetative body as by the relatively complicated sex organs of a type not found in any of the divisions already studied. These structures will be described in some detail later in this chapter.

The mosses are far more numerous and are somewhat more easily understood than the liverworts and for these reasons they are introduced first. The true mosses are a widespread group. They grow in almost all climates and habitats, with the exception that they are never found living in sea water. They live on the soil and on the bark of trees in tropical and temperate forests; they sometimes carpet fallow fields and sandy bars; a few species grow submerged in freshwater streams; still others associate with crustose and foliose lichens, building traces

of soil on dry rocks and lava beds where moisture sufficient for active growth is present for only brief periods after showers; some of them thrive best on the arctic and alpine tundras, where little else than a few lichens and dwarf woody plants can grow; and others invade areas newly made bare by forest fires.

The individual moss plants are always relatively small. In some species the total height does not exceed a fraction of an inch, while in others the plants may be a few inches tall. There is said to be a species in the Eastern Hemisphere south of the equator that sometimes attains a height of 15 or 20 inches, and it probably considerably exceeds all others in size.

The individuals of some species of moss grow packed together so closely that they form mats and cushions. These cushions sometimes cover areas several inches across, and occasionally attain a considerable depth. In mosses of this type the upper parts of the plants continue to grow upward while the older parts, which are nearer to the ground, die, forming a spongelike mass of humus. This decaying vegetable matter imbibes considerable amounts of water whenever rain falls. Sometimes there are sufficient numbers of these plants in forests to play a rather important role in retarding the runoff of water, causing it to soak into the ground, thereby reducing soil erosion.

Other mosses tend to stand somewhat apart like little weeds, while still others lie flat on the ground or on the bark of trees, often sprawling over considerable areas, especially in deep woods. While these types are probably less important than the cushion formers, they contribute somewhat to the production of humus.

Two orders of mosses will be discussed here. These are the true mosses (Bryales) and the bog mosses (Sphagnales).

THE TRUE MOSSES

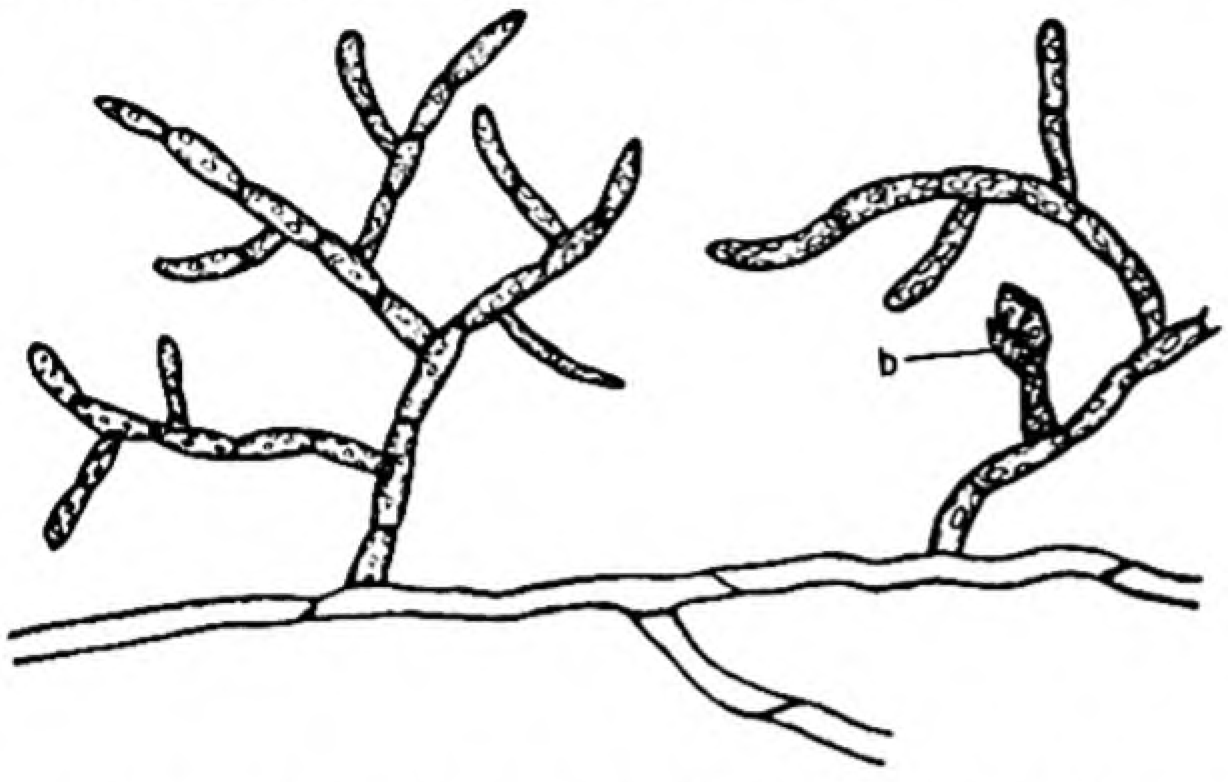
Organization. With the exception of minor details, such as size and growth habit, the great majority of the common mosses are so much alike that they are considered collectively rather than as individual genera and species. Because of their relatively large size, species belonging to such genera as *Polytrichum*, *Mnium*, *Funaria*, and *Catharinea* are most often examined by the beginning student.

The individual plant consists of a small, more or less wiry stem with thin, scalelike leaves forming a rather definite spiral around it. At its base, and sometimes elsewhere, fine, brown, hairlike threads, called *rhizoids* (*rhiza*, root; *oeides*, like) can be found. Under the microscope these are seen to be only one cell in thickness, and to be peculiar in that the transverse walls extend diagonally across them.

Moss plants showing stems with leaves and fine, hairlike rhizoids. (*Right*) Female gametophyte with sporophyte arising from its apex. (*Left*) Male gametophyte with cluster of antheridia surrounded by specialized rosette of leaves at its summit.

This leafy plant is the mature gametophyte gen-

eration. Upright, leafless stalks often grow up from some of the gametophytes. These are the sporophytes. On the top of each sporophyte there is commonly an enlargement, the *capsule*. Within the

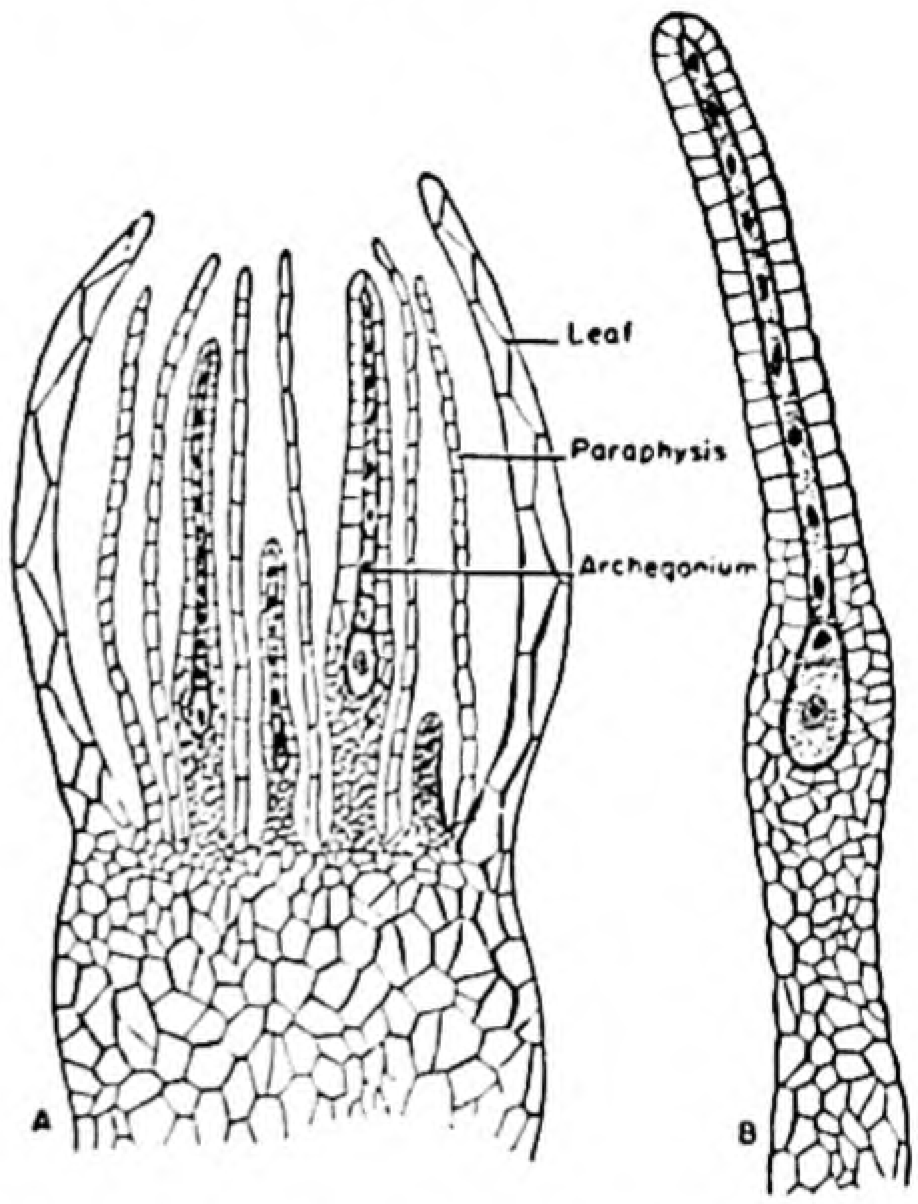


Moss protonema and rhizoid, showing characteristic diagonal cross walls in rhizoid below, and the alga-like, chlorophyll-bearing protonema above. (b) A young bud beginning to organize an upright, leafy plant.

capsule considerable numbers of spores are produced. The relations of the leafy gametophyte, the stalklike sporophyte, and the spores will become clear with the following discussion of the life history.

The Gametophyte Generation. The spore is the first cell of the gametophyte or haploid generation. When it germinates it gives rise to a small, green, branched thread that lies flat on the ground. This filamentous structure, called *protonema* (*protos*, first; *nema*, thread), when growing profusely on moist soil, may be mistaken for a growth of algae. In fact, even when protonema is examined with the microscope it has much the appearance of one of the branched septate Protochlorophyta.

The main body of the protonema is made up of filaments which are only one cell in width. After a time, however, thick, tuberlike green vertical stems are formed on some of the branches, and from these the leafy green plants develop. At the tip of each of these young shoots an inverted three-sided pyramidal *apical cell* is organized. Cells are cut off mitotically from these three sides in turn. These new cells form the mature parts, giving to the young plant a three-cornered shape and resulting in a more or less indefinite three-rowed arrangement of the leaves. At the base of the stems and on other parts of the plant which are protected from light, numerous small brownish rhizoids sometimes develop. If they are exposed to the light these branches become protonema. Likewise, branches of protonema that grow under ground become rhizoids.



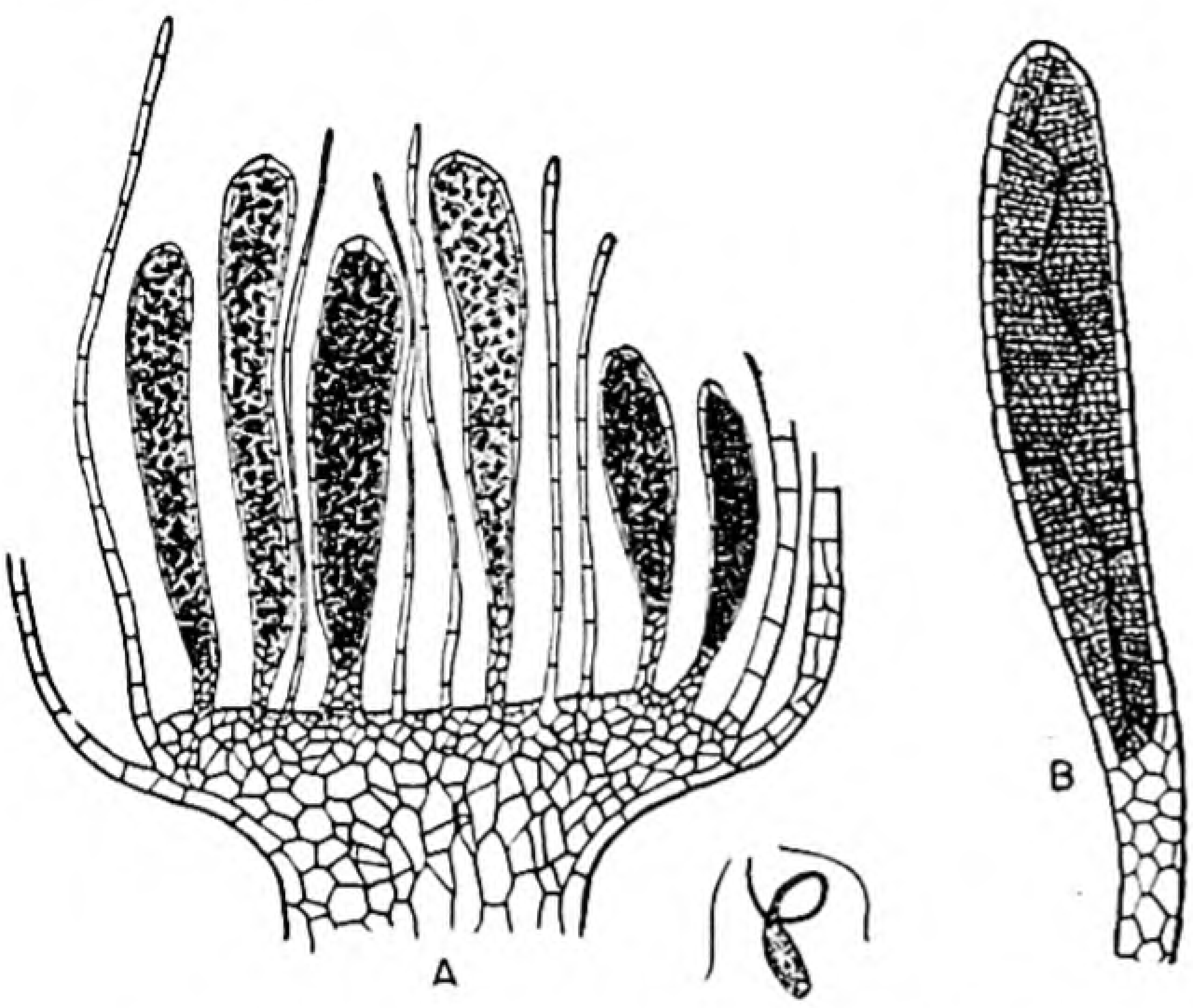
Moss archegonia. (A) Cluster of archegonia and paraphyses at top of female gametophyte. (B) Single archegonium containing egg (largest cell) in venter, above which is a ventral canal cell followed by numerous neck canal cells.

As in the algae and fungi, the structures that contain the sperms are called *antheridia*, but a new name, *archegonium* (plural, *archegonia*), applies to the container of an egg cell. Each archegonium contains an egg imbedded in its thick, fleshy base, called the *venter*. Above the egg, in the upper part of the venter, is a smaller, cone-shaped cell, the *ventral canal* cell. Beyond the venter is a long slender *neck* through which extends the *neck canal* which is filled with a single row of narrow *neck canal cells*.

The antheridium is also a rather complicated structure. When mature, it contains large numbers of sperms enclosed in a jacket constructed of numerous cells. These many-celled sex organs contrast markedly with their simpler counterparts, the antheridia and oögonia in the most primitive plant divisions.

In the genera usually studied in the laboratory the antheridia of male gametophytes and the archegonia of female gametophytes are grouped together at the tops of upright stems. Crowded in between them are numerous small threadlike

growths, the *paraphyses*. Immediately below the sex organs and paraphyses are usually a few leaves somewhat different in shape from the ordinary foliage leaves.



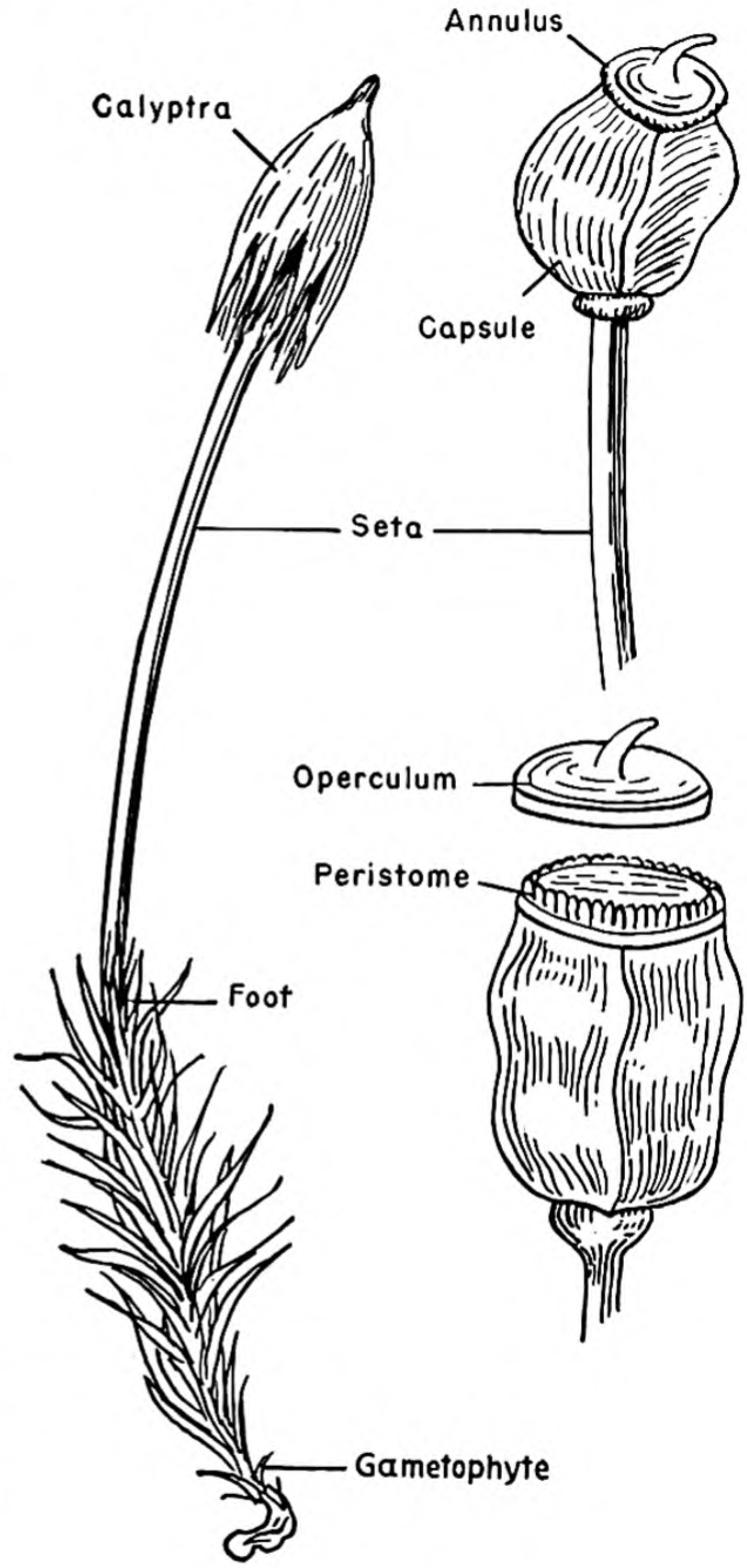
Moss antheridia. (A) Cluster of antheridia with slender paraphyses at top of male gametophyte. (B) Antheridium almost ready to produce sperms. (C) Coiled, biflagellate sperm, greatly magnified.

Fertilization. However dry the habitat, at this stage of its life history a moss becomes essentially aquatic, for without rain or a heavy dew fertilization fails to occur. When an archeogonium is mature the neck canal cells disorganize into a mucilaginous mass of material which absorbs water and swells, bursting the top of the archegonial neck. In a similar manner the mature antheridia absorb water and burst, liberating the sperms.

The sperms are very small and can be observed satisfactorily only with high magnification. Each consists of a slender, coiled body and a terminal pair of flagella. Here, again, *Chlamydomonas*-like cells occur, indicating a relationship with such Protochlorophyta as *Ulothrix* and its relatives.

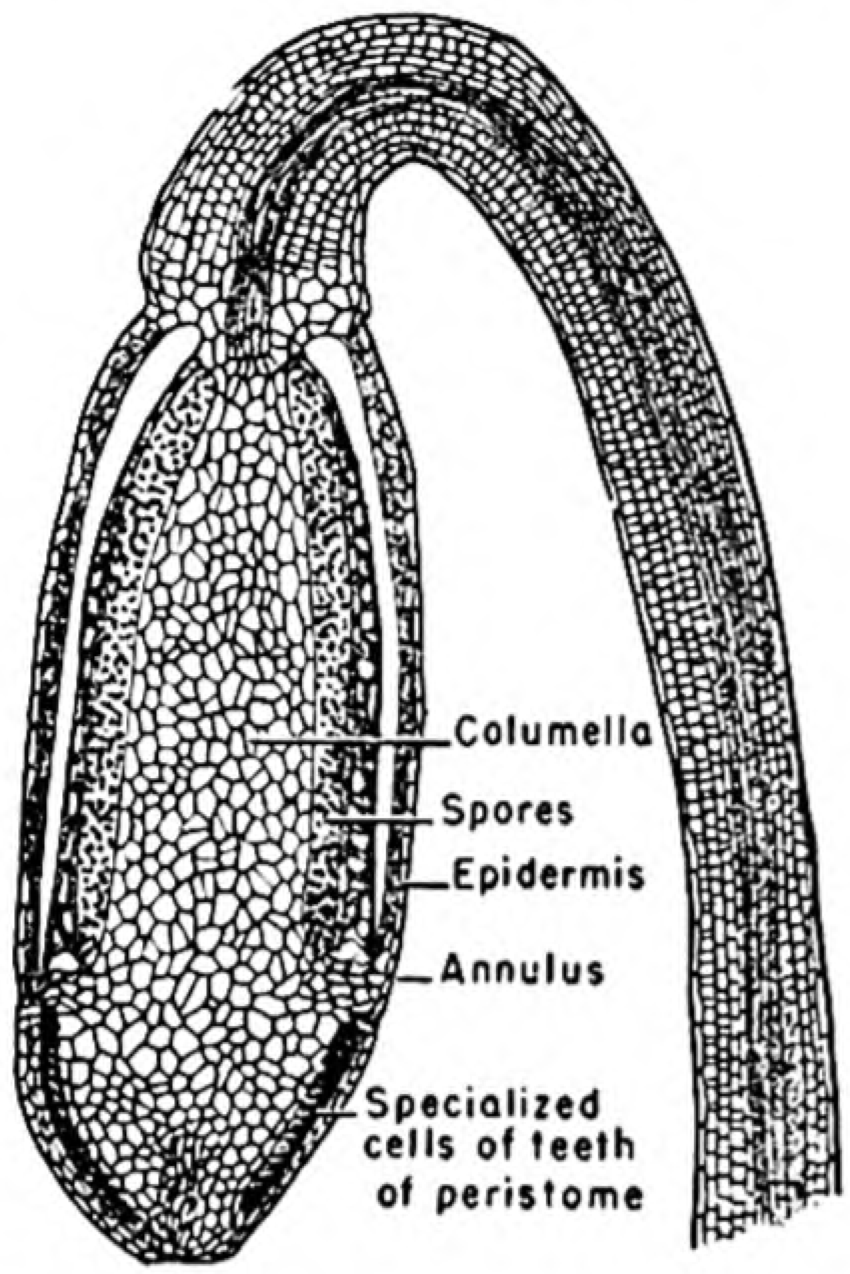
When the sperms have escaped from the ruptured antheridium they swim in such water as may be present on the surface of the plants until they reach the archegonial neck. Then they travel through the neck canal to the egg where one of them unites with it in the usual way. They have a decided positive chemotactic response to sucrose. Laboratory experimentation has shown that they are definitely attracted to as dilute a solution of this sugar as 0.001%. Presumably this is the means by which they are directed to the egg.

The Sporophyte Generation. Both the sperm and egg are haploid cells. When they unite they produce a diploid zygote—the first cell of the sporophyte generation. By a series of rapid divisions this fertilized egg gives rise to a small mass of cells, the immature sporophyte, enclosed in the



Moss sporophyte.

growing venter of the archegonium. At length, the lower part becomes organized into a specialized absorptive organ called the *foot* Later, the portion above the foot elongates greatly, forming a slender



Moss capsule showing internal structure. This is the nodding type of capsule. At right is the seta.

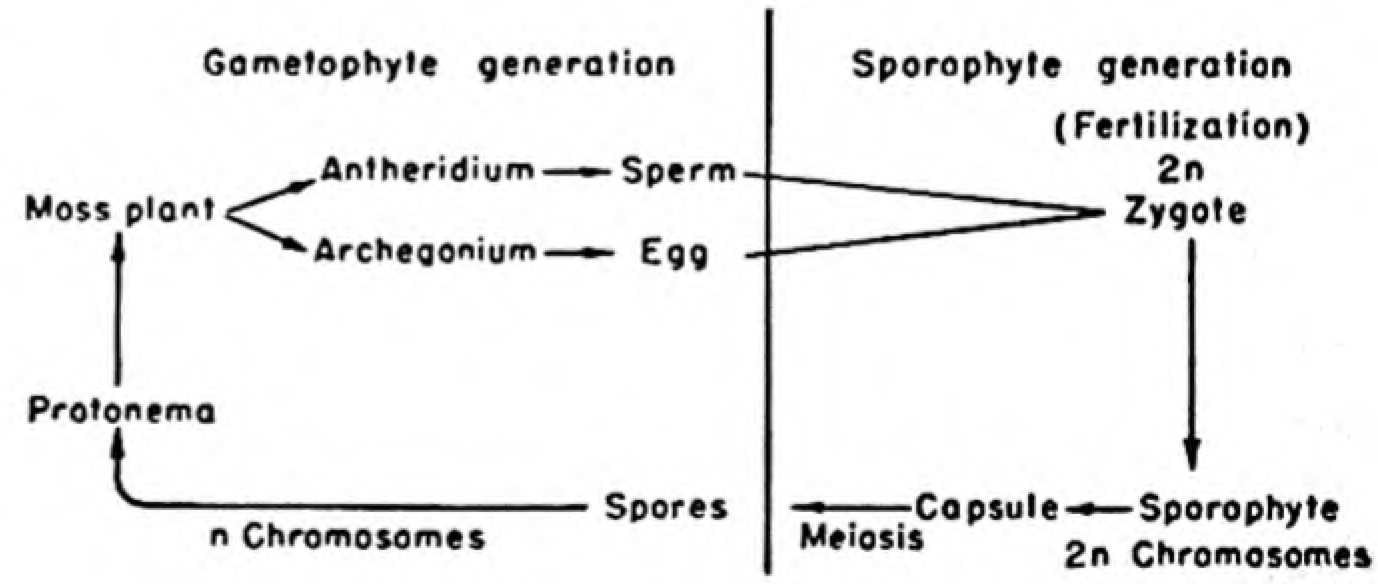
stalk, the *seta*, which is topped by an enlargement, called the *capsule*. The upward thrust of the growing seta forces the foot and capsule farther apart, in this way tearing the upper part from the archegonium and wedging it onto the top of the capsule. This old archegonium wall is called the *calyptra* (*kalyptra*, a cap). Although the calyptra remains like a cap on top of the capsule, it is not a part of the sporophyte but is a piece torn from the gametophyte by the growth of the sporophyte.

It is frequently possible to remove the foot from its place of anchorage in the end of the leafy gametophyte in such a way as to make it evident that it was not definitely attached but rather was set in a depression in the end of the leafy stem. The foot is an organ of absorption, water and nutrients being taken through it from the gametophyte. In other words, the moss sporophyte acts as a parasite on the gametophyte.

By slightly magnifying the upper part of a mature sporophyte it is possible to make an instructive dissection. After removing the calyptra—a tattered cap of gametophytic tissue—an examination of the bare capsule reveals a constriction, called the *annulus* (*annulus*, a ring), near its upper end. The annulus is composed of a ring of tissues so constructed that they tend to break apart when they become dry, allowing a caplike upper portion, the *operculum*, to fall off.

Removing the operculum and magnifying the mouthlike opening of the capsule shows a circle of from four to many toothlike projections with their free ends pointing toward the center. These are the teeth of the *peristome* (*peri*, around; *stoma*, mouth). These teeth are usually constructed of cell walls only, the protoplasm disappearing as soon as the walls have been formed. Because of a peculiar arrangement of the layers of materials that form the teeth, they tend to open outward when they become dry and to close in against each other when they are moist. This mechanism permits the spores to be shed at times when they can be carried about by wind action like dry grains of dust, but holds them in the capsule during rainy periods.

Thin sections cut longitudinally and transversely through capsules and properly stained to show internal structures give still more information. At the center there is a shaft of parenchyma, called the *columella*. Immediately around the columella is a zone of sporogenous, that is to say spore-produc-



Life history of moss.

ing, tissue. If the capsule is almost mature this tissue may have already changed into spores. Around this part is a zone of cells with many intercellular spaces. Many of these cells contain chlorophyll. Enclosing all the other parts is an epidermis

with stomata much like those of the stems and leaves of higher plants. Throughout the plant kingdom stomata with guard cells are found only in the sporophyte generation. These stomata act as channels of communication between the outer air and the intercellular spaces, making possible the exchanges of gases that take place in such processes as photosynthesis and respiration.

Alternation of Generations. The sporophyte generation begins with the zygote with its diploid number of chromosomes, and continues to the point at which spores are formed. The spore mother-cells, which constitute the sporogenous tissue, grow rapidly at the expense of a nutritive tissue called the *tapetum*, which surrounds them. Each finally undergoes the characteristic meiotic divisions, forming a tetrad of haploid spores. The spore, as usual, is the first cell of the gametophyte generation, and the protonema, the leafy plant, the rhizoids, the sex organs and the gametes are haploid. With the union of two haploid gametes the diploid zygote is formed, completing the cycle.

THE BOG MOSSES

The genus *Sphagnum* is commonly known as bog moss. The various species belonging to this genus are to be found in wet places, such as swamps, ponds, and quiet lakes of the cooler parts of Europe and North America. Bog moss is especially likely to thrive in places where there is very little lime in the soil and where the water, therefore, tends to be somewhat acid. The common name refers to the fact that this plant is a usual important component of the vegetation that grows in peat bogs. The peculiar part it plays in bog formation will become apparent in succeeding paragraphs.

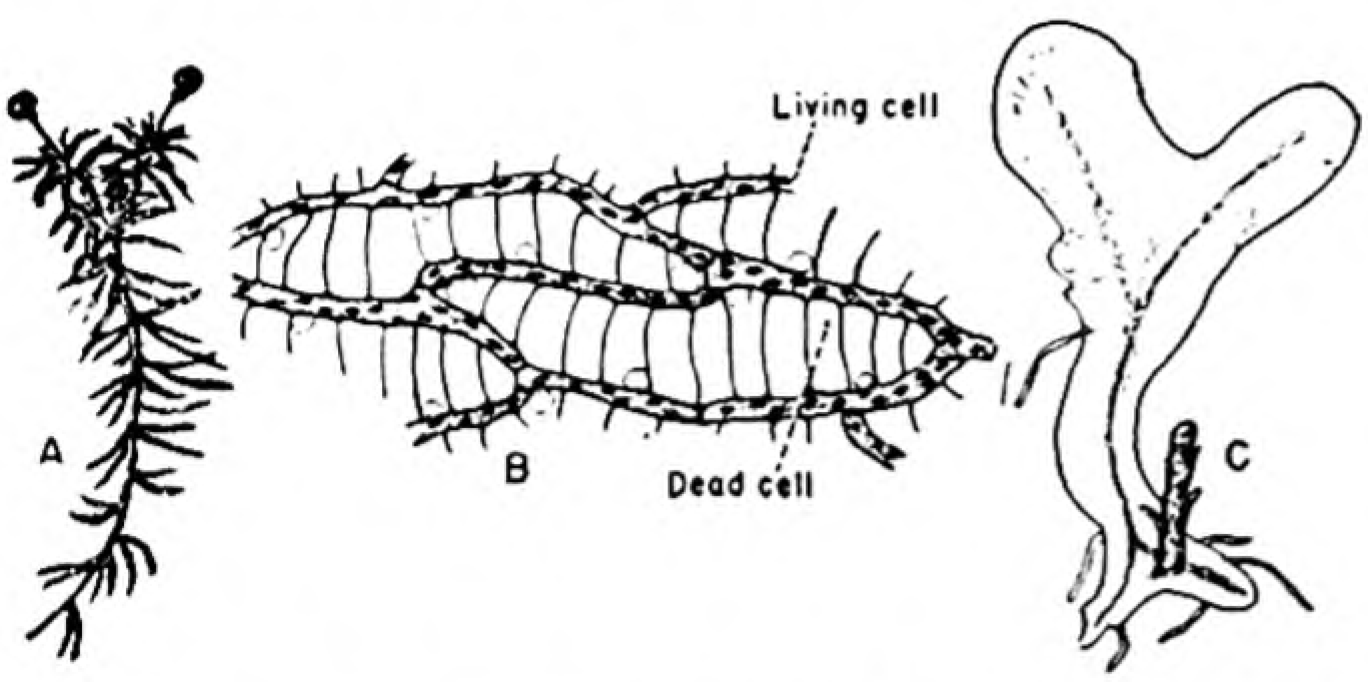
This moss usually grows in the form of extensive mats or cushions, even spreading over floating debris at the margins of ponds or lakes or attaching itself to shore vegetation, gradually extending as a thick, spongelike carpet over the water.

Such a floating surface affords a suitable propagation center for a considerable number of the higher plants. Among these are cranberries, cattails, bulrushes, certain ferns, and even tamarack and other trees. Many of these plants have extensively branched rhizome systems which, with their roots, form a firm mat. In this way, *Sphagnum* is given support while it, itself, makes a sort of living soil in which roots and rhizomes are imbedded. This entire floating structure constitutes a peat bog.

As these plants grow they become heavier. Usually the upper ends of the shoots continue to live and elongate while the older, lower parts die as the

Peat bog. The floating bog is the flat portion in the foreground. The background is the edge of a forest on surrounding higher ground. *Sphagnum* is an abundant part of the bog flora.

weight above them forces them below the water surface. Under these conditions the oxygen dissolved in the water is rapidly depleted and the aerobic bacteria of decay do not thrive. Therefore,



Sphagnum. (A) Gametophyte with two sporophytes at upper end. (B) Cellular structure of leaf. Living cells contain chlorophyll; dead cells act as water storage compartment. Note pores in walls. (C) Broad, flat protonema with young, upright leafy branch forming. Note threadlike rhizoids.

the submerged parts of the plants disintegrate immeasurably slowly. Even spores, pollen grains, and other delicate cells are sometimes so well preserved that they can be recognized with little difficulty after they have been buried in a peat bog for thousands of years.

This miscellaneous collection of slightly decomposed plant tissues constitutes peat. Old bogs may finally deposit such large amounts of peat that entire lake beds are completely filled. In the northern part of the United States and in Canada there are today extensive forests rooted in beds of peat that gradually formed in the cold lakes and ponds of past centuries. Older bogs in which the peat has decayed, forming humus, are often productive farms. When extensive supplies of peat become compacted and relatively dry they form a great source of potential fuel. Even today, in some parts of Europe where coal and wood are not easily available, peat is burned in large quantities.

The Gametophyte. As in other mosses, when spores germinate they produce a green structure commonly called the protonema. In the bog mosses, however, the protonema assumes a broad, flat form and from it arise the buds that develop into leafy plants. As is usual, the spore is the first cell of the gametophyte generation, and the protonema and leafy shoots are the later stages in its development.

In many respects sphagnum resembles true mosses but it is markedly pale green in comparison with most of them. The reason becomes evident when the leaves of bog moss are examined with the microscope. The mature leaf is made up of slender chlorophyll-bearing cells arranged in a network whose meshes are filled with large, colorless, hollow walls from which the protoplasm has disappeared. The diluting effect of these microscopic areas in the green background of the leaf accounts for its pale color.

These empty cell walls act as water reservoirs. Their collapse is prevented by spiral or annular thickenings, and small pores permit the ready entrance of water from the outside. Because of this peculiar structure, a mass of this moss, whether alive or dry, has remarkable absorbent capacity. In fact, dry sphagnum is said to absorb about 200 times its own weight in water. For this reason water can usually be squeezed out of living bog moss almost as from a wet sponge, and the wicklike action of this plant even permits it at times to grow up hillsides, receiving its moisture from the margin of a floating bog.

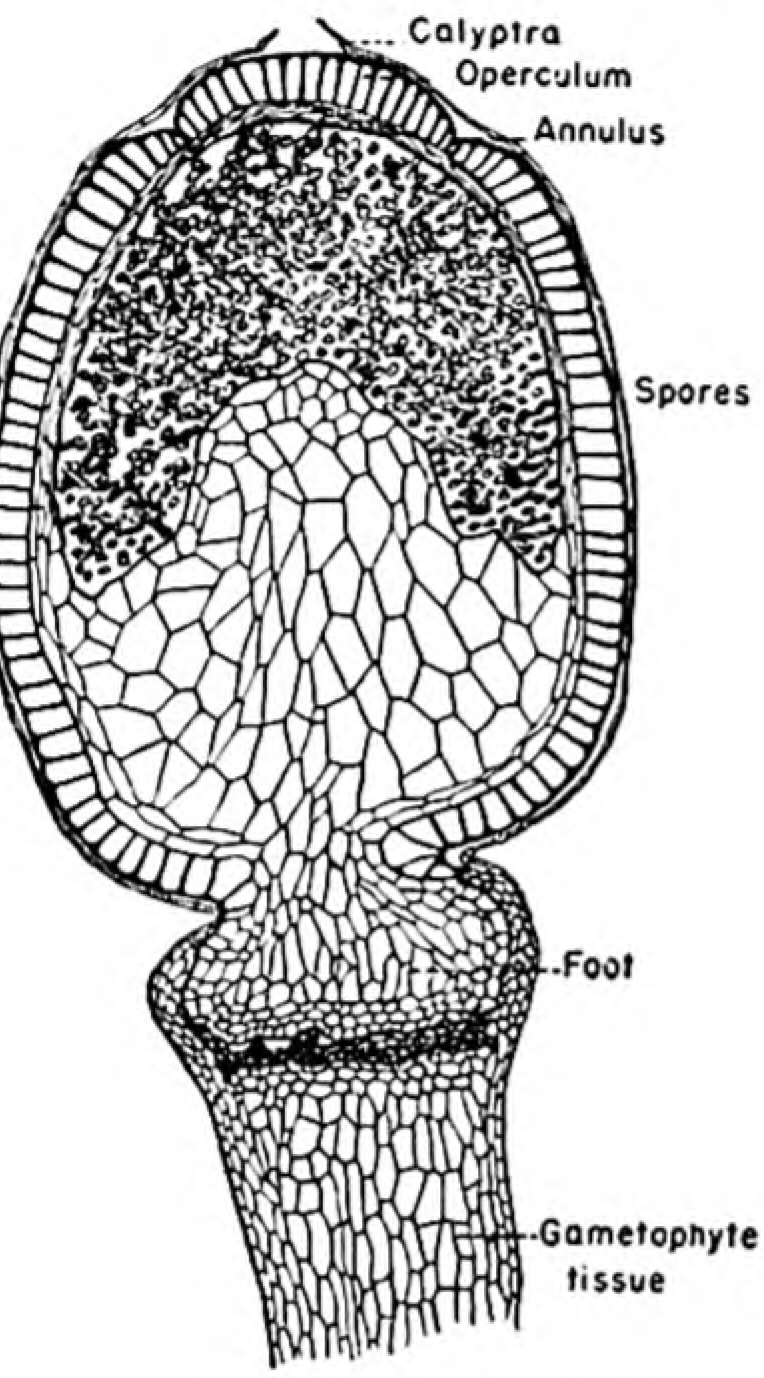
The great absorbent power of sphagnum gives it an important commercial value. Nurserymen have long used large quantities to protect the roots of trees and other plants from drying during transportation. As soon as the roots are removed from the soil they are quickly covered with wet moss and then are securely wrapped. With this kind of care they remain moist for several days or sometimes for a few weeks.

This same ability to absorb large amounts of liquid has, within recent times, made bog moss highly valuable in the preparation of surgical dressings. In some ways it makes a more satisfactory means of stopping blood flow than the usual gauze and absorbent cotton.

As in other mosses the mature leafy plant belongs to the gametophyte generation. At certain times, therefore, it may organize antheridia and archegonia. These form at the tips of leafy plants, some

species being monoecious and others dioecious. Fertilization is much the same as in other mosses.

The Sporophyte. The structure which develops following fertilization is somewhat confusing. A rounded body forms, perched on a slender stalk. (See p. 270 and also the accompanying illustration.)



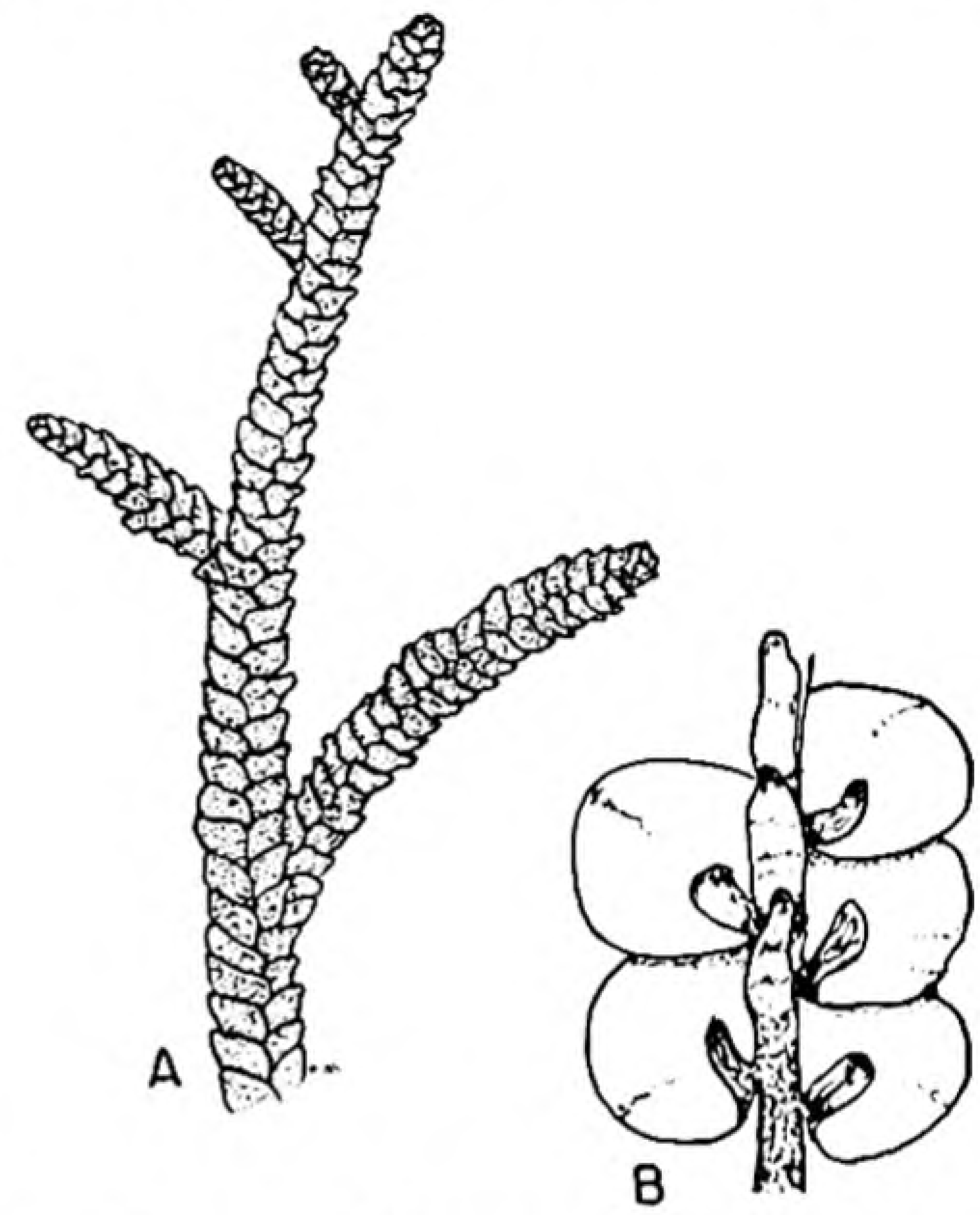
Sporophyte of *Sphagnum*. The gametophyte tissue has elongated into a stalk, the pseudopodium, which holds the sporophyte above the main level of the leafy plant.

The general appearance is much like that of the sporophyte of an ordinary moss but microscopic sections cut lengthwise show that the stalk, called the *pseudopodium*, is an outgrowth of the leafy gametophyte, and the globular body at the top is a sporophyte with a very short seta and a well-developed foot embedded in gametophytic tissue. With the exception of the foot the sporophyte is entirely encased in the greatly enlarged venter of the archegonium. As in the true mosses this archegonial wrapping is called the calyptra.

The structure of the sporophyte is simpler than that of ordinary mosses. There is an operculum, as usual, but the sporogenous cells form a dome-shaped mass. Rudimentary stomata are present, but the elaborate differentiation of the vegetative tissues seen in other mosses, is lacking. The formation of the spores includes the ordinary reduction division and introduces the gametophyte generation.

THE LIVERWORTS

The Hepaticae are a somewhat more primitive group of bryophytes than the Musci. A few of them



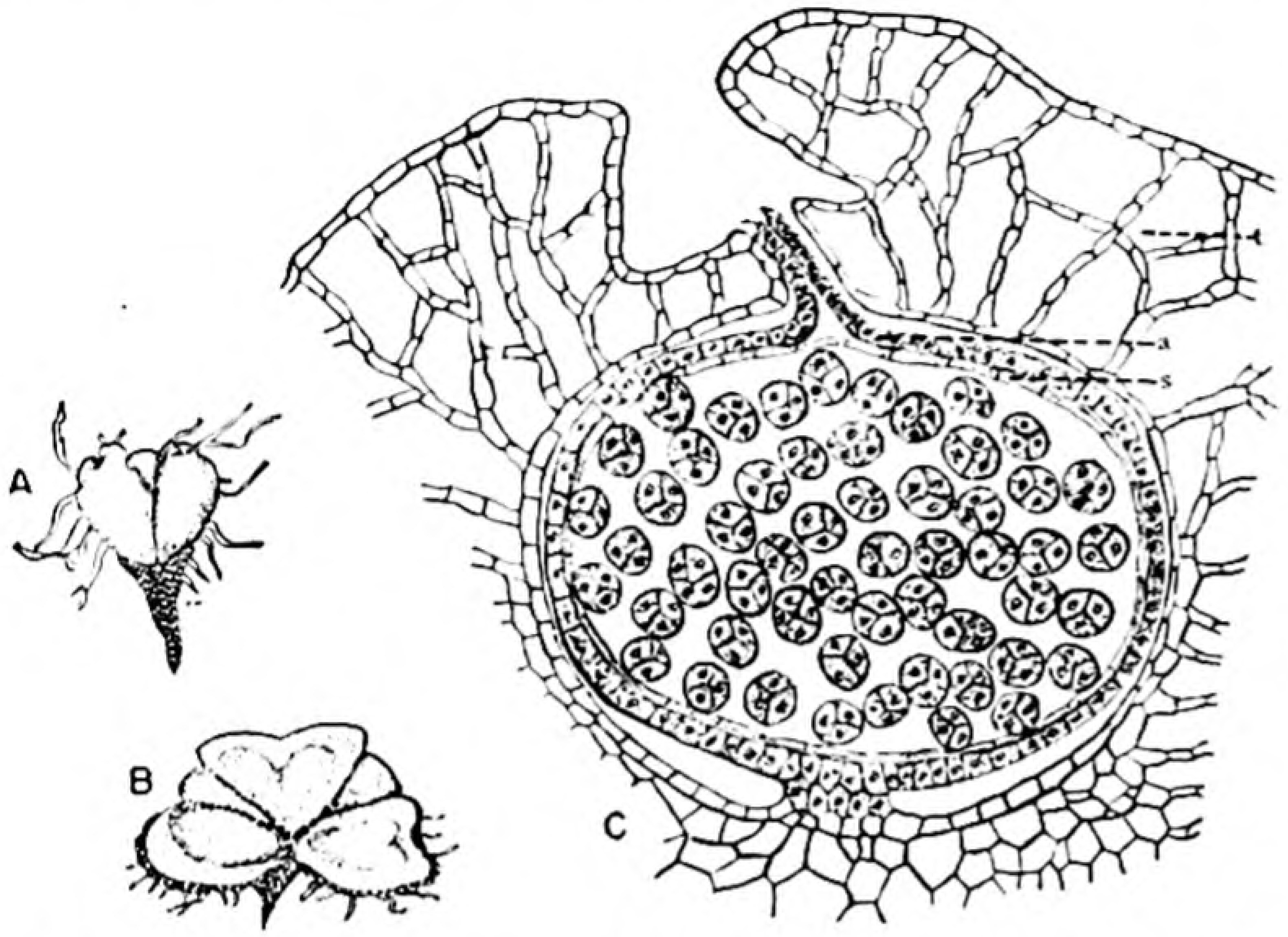
Porella, a leafy liverwort. (A) Dorsal or top view. (B) Ventral view showing three amphigastria largely covering the stem, and five leaves, each with its ventral lobe.

resemble the mosses to a considerable extent. A representative of these leafy, mosslike liverworts will, therefore, be introduced at this point.

A Leafy Liverwort. Some species of liverworts have leafy stems and so closely resemble mosses that the difference can be detected only on careful examination. These leafy species are numerous and difficult to distinguish from each other. *Porella* is a genus that is representative and widely distributed, growing on rocks, logs, and tree trunks, and sometimes even in water.

The gametophyte resembles a prostrate, branching moss plant but, it is definitely *dorsiventral*, that is, the upper side is different from the lower. From above, it seems to have two rows of leaves, but examination of the lower side reveals an additional row of small, rudimentary ones, called *amphigastria*. Small lobes of the large leaves sometimes lap over the lower surface of the stem in such a way as to

prove confusing, but their real nature becomes evident when a leaf is removed from the stem. The suppressed development of one of the three rows in the leafy liverwort is one of the clearest marks of distinction between it and a moss. One other difference is that the leaf of the liverwort shows no indication of a midrib, while that of a moss usually has a thickening extending throughout its length, giving the impression of one.



Riccia. (A) Young gametophyte with rhizoids and a scale. (B) Mature gametophyte with numerous sporophytes in the grooves. (C) Sporophyte as seen in section; (t) tissue of gametophyte; (a) archegonium wall; (s) wall of sporophyte enclosing tetrads of spores.

The archegonia are borne on small, budlike branches along the stem of the plant. The antheridia are produced in short, compact shoots which are less differentiated than those bearing archegonia. In the commoner species the plants are dioecious, and large unisexual colonies are frequently found. The sex organs are not essentially different from those of mosses, and fertilization is equally dependent on moisture.

The sporophyte consists of a round capsule borne on a short seta, and the foot is imbedded in the tissue of the gametophyte. The capsule usually splits open by a more or less definite number of valves. It is filled with spores and *elaters*, the latter being peculiar long cells with spiral thickenings on their walls. The elaters are very sensitive to changes in moisture and, although dead, when released from the capsule they may be seen to writhe and twist in a lifelike manner as they absorb or lose water. They may facilitate the distribution of the spores by loosening the mass when the capsule breaks open, but there is little evidence of any significant or important function.

Thallose Liverworts. The name, thallus, is applied frequently to any undifferentiated or slightly specialized plant body. Consequently, the expression, thallose liverworts, is applied to a group of the Hepaticae that have flat, dorsiventral bodies but are entirely devoid of stems and leaflike structures. These liverworts do not have a mosslike appearance.

RICCIA. The various species of this genus float in water or grow on moist soil, as on the mud around ponds. The gametophyte is usually a thick, flat, branched, wedge-shaped or almost circular thallus. The lower side sometimes bears thin scalelike appendages which have been interpreted as vestigial leaves. Rhizoids also may be present. The upper part of the thallus is made porous and spongy by numerous air spaces which have the same significance as the spaces in the mesophyll of a leaf.

The antheridia and archegonia are located in considerable numbers in grooves in the upper surface of the gametophyte. After fertilization, the sporophytes develop as spherical bodies within the groove of the thallus. When mature, a sporophyte consists of only a thin wall and a mass of spores. The latter are set free by the decay of the thallus and develop directly into new gametophytes. No liverwort has a simpler sporophyte than this.

MARCHANTIA. One of the most conspicuous and best known of all liverworts is *Marchantia*. Large quantities of this plant, or of other genera so much like it as not to be readily distinguished from it, are to be found on shaded cliffs, on wet rocks along streams, on damp soil in shady places, and under the benches of greenhouses. It grows frequently


Marchantia. (*Right*) Gametophyte with gemmae. (*Left*) Crowded plants with antheridial heads (wheel shaped) and archegonial heads with sporophytes (umbrella shaped).

on soil which has been burned over, although it is by no means limited to this kind of habitat.

THE GAMETOPHYTE. The thallus is often large and vigorous and considerable areas of soil are sometimes covered two or more layers deep at the close of a good growing season. The thick, flat segments branch dichotomously again and again, that is, they tend to fork repeatedly into two equal branches. As in most thalloid plants of this type, growth at one end is accompanied by the slow dying of the other, thus producing two new plants at each fork.

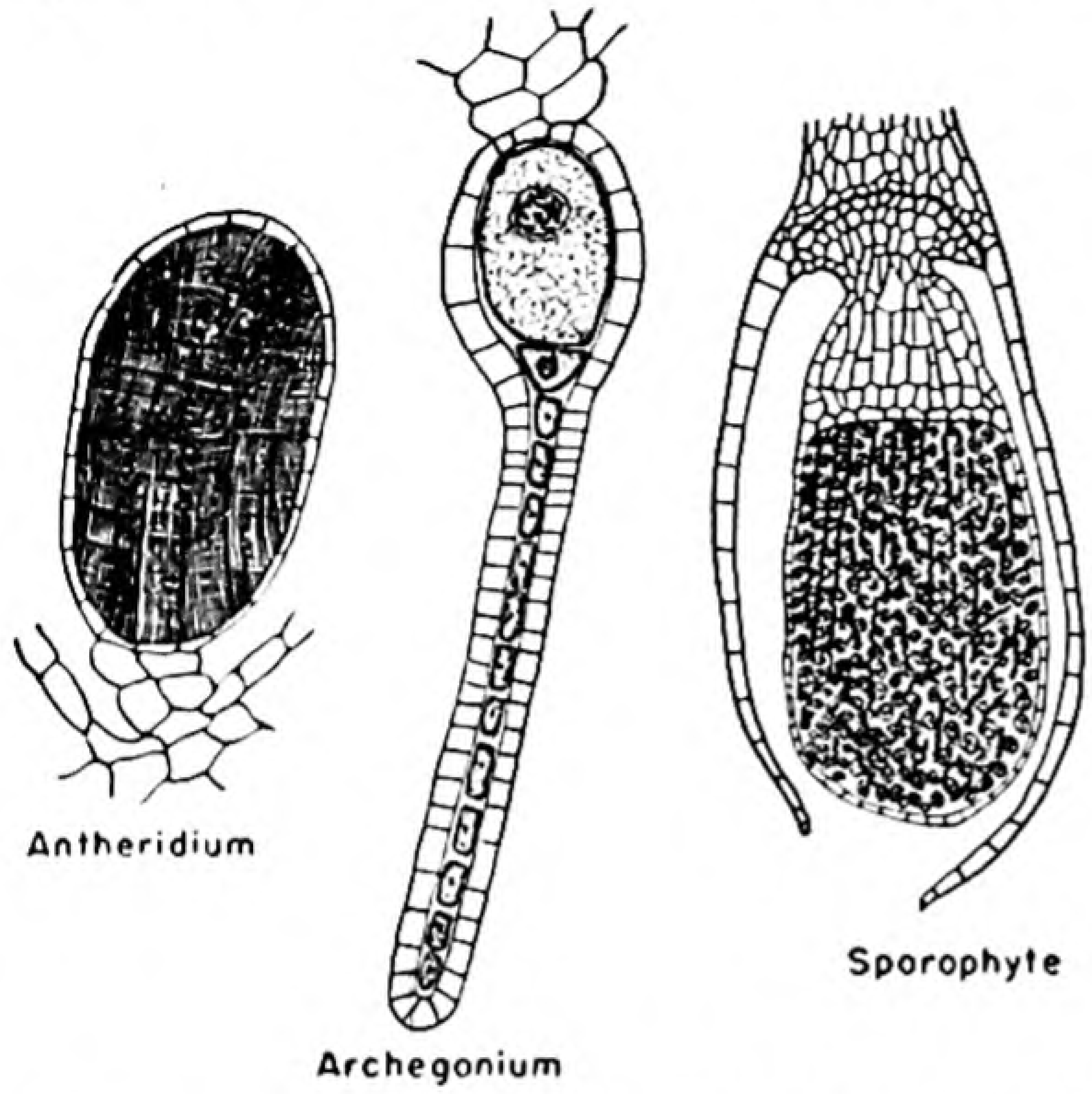
The upper epidermis of the thallus is marked off into small, elevated, polygonal areas, each having a tiny pore at its center. These areas are really the covers of a series of subepidermal cavities whose boundaries are immediately over the walls which enclose these spaces. The chlorophyll-bearing tissue of the thallus consists largely of a mass of erect microscopic cactuslike growths standing up in these cavities. Gaseous exchanges with the outer air, such as those that take place in photosynthesis and respiration, are brought about by diffusion through the pores. On the lower surface of the thallus are numerous rhizoids.

The plant propagates itself very efficiently by simply growing, but wider dispersal is brought about by special structures known as *gemmae*, which are borne in considerable numbers in cuplike structures on the upper surface of the thallus. Each gemma is a minute, thickened, flat, almost circular outgrowth from the bottom of the cup. When mature it is easily broken off and washed out by rain. Both surfaces are alike at this time, but as soon as it falls on the soil and begins to grow, it develops the characteristic dorsiventral structure of the adult thallus.

The antheridia and archegonia are produced in conspicuous, highly specialized structures which stand high above the surface of the thallus. The plants are dioecious, that is, separate male and female gametophytes occur. The archegoniophore (*pherein*, to bear) consists of a number of fingerlike, radiating branches borne at the top of a long stalk. The archegonia hang from the lower side in the notches between the branches. The antheridiophore is a lobed disk borne on a somewhat shorter stalk. The antheridia are imbedded in cavities in the top of the disk.

Except for the impressive journey which the sperm must make in traveling in a film of water from the antheridium of the male gametophyte to the archegonium of the female, fertilization is not unlike that in other bryophytes.

THE SPOROPHYTE. The sporophyte develops for a time inside the archegonium. A foot acts as an absorptive organ and a seta forms between it and the capsule. Within the capsule the majority of the



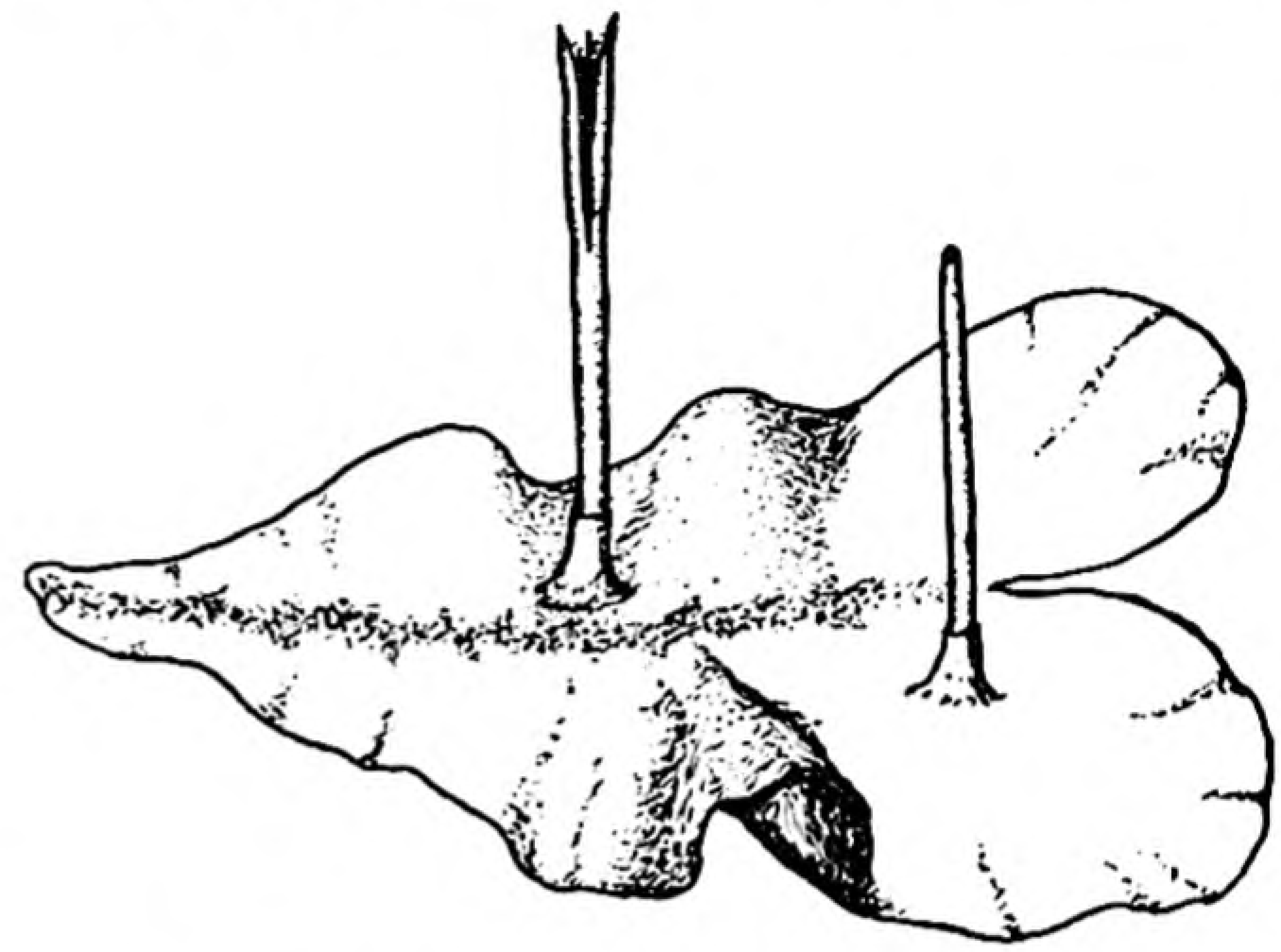
Antheridium, archegonium, and sporophyte of *Marchantia*.

spore mother-cells give rise to spores by meiotic division, and the remainder change into elaters. When mature, the capsule breaks open and the seta elongates sufficiently to permit the spores to be caught up by the wind. Those that chance to fall into suitable places grow directly into new gametophytes.

ANTHOCEROS. In many respects *Anthoceros* and its relatives stand apart from the other liverworts. The gametophyte is a simple, thin, flat or wrinkled thallus. The sex organs and the process of fertilization present no significant features not already encountered, except that the archegonium is sunken in the tissue of the gametophyte. This characteristic is common in the higher plant groups next to be studied.

It is in the sporophyte, however, that *Anthoceros* deviates most widely from prevailing patterns. This is an erect, pointed horn-shaped structure often more than an inch tall. Its peculiar appearance is responsible for the common name of "hornwort" which is frequently applied to these plants. It is comparatively uniform in diameter and, although there is no differentiation into capsule and seta, it is highly specialized in other respects.

The spore-producing tissue is in the form of a hollow cylinder with a central columella which suggests a very simple stele. A section near the base of the sporophyte remains meristematic, continuing



Anthoceros gametophyte with two sporophytes attached.

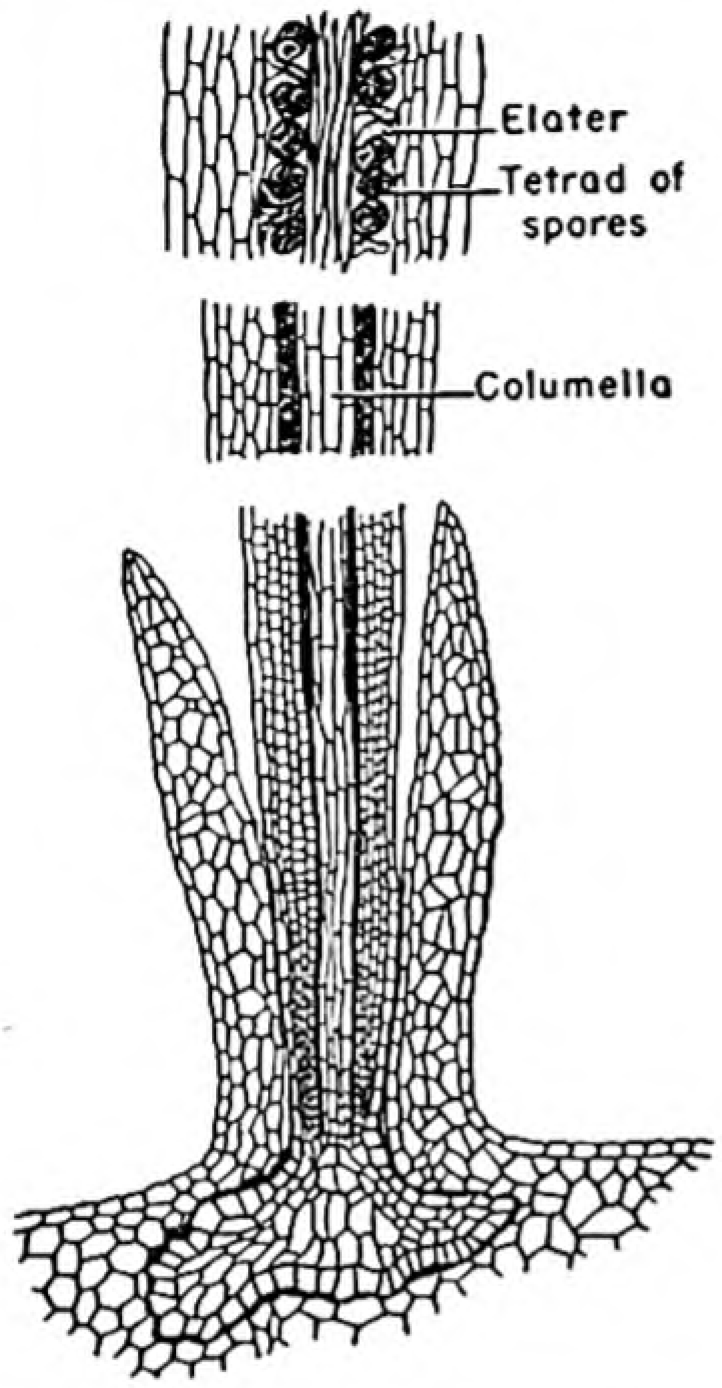
to elongate indefinitely. Differentiation occurs upward, and sporogenous tissue organizes, giving rise to rudimentary elaters and tetrads of spores. These mature, and are shed through a split at the top.

A massive foot imbeds itself in the gametophyte. In some species the foot is so highly developed that it almost breaks through, nearly establishing direct, rootlike contact with the soil. A sheath grows up from the gametophyte, providing mechanical reinforcement for the meristematic lower part of the sporophyte. The cortexlike tissue outside the sporogenous region is well supplied with chloroplasts, and stomata similar to those of higher plants are present in the epidermis. Therefore, it is probable that the sporophyte makes a significant amount of food for itself, almost becoming an independent plant.

Relationships of the Bryophytes. In attempts to discover the ancestral groups from which various kinds of organisms have evolved, search is usually made for evidences derived from fossils. In the case of bryophytes, however, such evidences have been very limited. The most ancient fossils of both liverworts and mosses that have been discovered came from the carboniferous period (see p. 169). These, however, are not of such nature as to indicate their relationships with any other group. For

this reason, it is necessary to depend for the present on interpretations of the structure and form of modern bryophytes in reaching tentative conclusions.

The following discussion outlines the evidences



Anthoceros sporophyte as seen in longitudinal section. At the base, and extending up the sides for some distance is a part of the gametophyte.

now available. Exactly the same sets of pigments are universal in the Protochlorophyta and in the Bryophyta. This is strong presumptive evidence of actual genetic relationship. But there are many variations among the different groups of green algae, and it would seem probable that the Bryophyta might show greater hereditary similarity to one of these groups than to others. *Vaucheria* and its relatives can be immediately eliminated because they are coenocytes and all the bryophytes are definitely septate in structure; likewise, *Oedogonium* can be passed over because of its numerous flagella arranged in the form of a crown in all its swimming cells, including both sperms and zoöspores; and, finally, *Spirogyra*, together with the entire order to which it belongs, has no flagella at any time in its life history. In addition, all members of this order have very peculiar chloroplasts that are entirely different from any that are found in higher plants.

In contrast with the members of these various algal groups, all of the Bryophyta have terminally biflagellate sperms, strongly suggesting the *Chlamydomonas*-like cells which are so much in evidence in certain of the filamentous algae. It is true that these bryophyte sperms are long, narrow, and somewhat curved, but their general structure seems to be only slightly modified from that of those more primitive forms. Again, the protonema of true moss especially suggests filamentous algae, and this is often interpreted as indicating a probable relationship with them.

When all sets of characteristics are taken into consideration, many botanists reach the conclusion that the ancient, algal ancestors of Bryophyta must have been something like modern *Ulothrix* or some of its near relatives. No one would suggest that *Ulothrix* or any other living alga was the forerunner of the bryophytes. Rather, it would seem that the gene combinations nesessary to produce the characteristic pigments, sperms, and general cellular structure have probably been handed down in both lines of descent with only slight deviations from some ancient alga which possessed these hereditary traits.

If this interpretation is correct, the greatest changes which have occurred in the evolution of the Bryophyta have been those bringing about the development of the somewhat complex sex organs, the more highly organized gametophytes, and a considerable advance in the sporophyte.

The variations which have become important within the Bryophyta have followed two lines of specialization, producing the two classes within this division. These classes are:

Hepaticae, the liverworts, including the leafy liverworts, and *Riccia*, *Marchantia*, and *Anthoceros*.

Musci, the mosses, including both *Sphagnum*, order Sphagnales, and the "true mosses," order Bryales.

SUPPLEMENTARY READINGS

Campbell, "Mosses and Ferns."
Conard, "How to Know the Mosses."
Grout, "Mosses with a Handlens."
Smith, "Cryptogamic Botany." Vol. II.

Chapter 18

PSILOPSIDA, SPHENOPSIDA, AND LYCOPSIDA

This chapter, besides contributing information concerning some common plants of the present time and their ancient forebears also lays a foundation for subsequent discussions.

The following table of the Paleozoic Era is a brief summary of the geologic record as it relates to the early evolution of vascular plants. A careful study of this table makes it clear that after the first of these plants had appeared in the Silurian Period, new groups came into existence with remarkable rapidity during the succeeding Devonian Period—the most exciting time in all the history of plants!

PALEOZOIC ERA*

Period (Each number refers to the approximate number of millions of years from the present back to the beginning of the period)	*Plant Life*
Permian 225	Small remnants left of each of the great groups
Pennsylvanian 270 and Mississippian 300	Lycopsida, Sphenopsida, and Cycadofilicales reach their climax and begin to die out
Devonian 345	Lycopsida, Sphenopsida, ferns, and Cycadofilicales appear and Psilopsida disappear
Silurian 375	First Psilopsida Algae
Ordovician 435	Algae
Cambrian 540	Algae

Read up from bottom (also see p. 169)

* Much of this material is adapted from Darrah: "Textbook of Paleobotany."

Outline of the chapter:

- Psilopsida
  - *Rhynia*
  - *Psilotum*
- Sphenopsida
  - *Equisetum*
  - Ancient Sphenopsida
- Lycopsida
  - *Lycopodium*
  - *Selaginella*
  - *Isoetes*
  - Ancient Lycopsida
  - *Asteroxylon*

The first xylem on earth seems to have appeared about 350 or 360 million years ago. The earliest fossil record of a plant with woody tissue thus far discovered came from deposits laid down in late Silurian times. By the beginning of the Devonian period several other, but rather similar, groups of plants had arisen. Fossils belonging to this group have been discovered in such widely scattered places as Wyoming, southeastern Canada, northern Europe, and even China and Australia. Such extended distribution indicates that this type of primitive land plant had already been in existence for a considerable period of time before the Devonian.

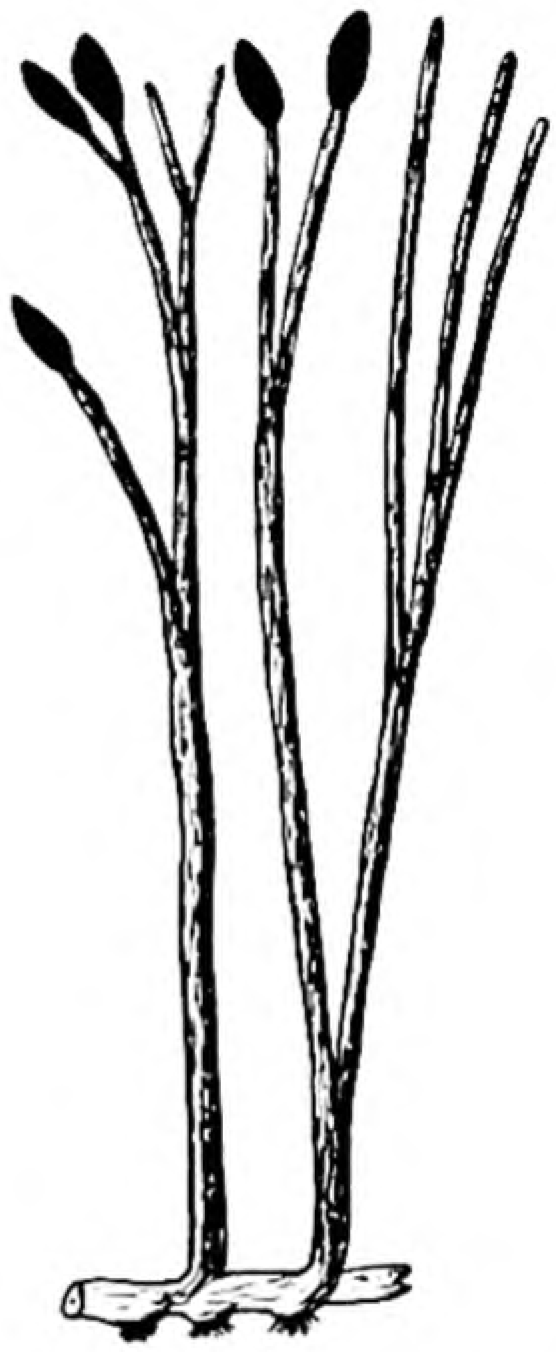
So far as evidences prove, the most complex plant life that existed before these new types originated was a considerable array of algal forms. Although the fossils of algae give little help in interpreting the alternation of generations in those ancient times, it seems safe to assume that the conspicuous plant bodies were gametophytes, at least in the majority of cases. This assumption is based on a knowledge of the life histories of present-day green algae. In these plants the gametophyte is usually the more prominent of the two generations, the sporophyte being only a single cell, the zygote, or occasionally a small, slightly more elaborate structure.

In studying the lower divisions of modern plants very little indication of conductive systems is found. In fact, there is no well-developed vascular tissue in any modern gametophyte. The nearest approach to it occurs in the stems of the mosses. Xylem and phloem are strictly sporophyte structures.

PSILOPSIDA

Those earliest fossil plants that had xylem in their stems, together with a few very similar forms that are still living in the tropics and subtropics, constitute this division of the plant kingdom.

Rhynia. Some of the simplest of the Devonian species belong to the genus, *Rhynia*. The sporophyte of this plant was a slender horizontal rhizome with leafless, upright aerial shoots. The name *Rhynia* was given these fossil plants because they were discovered near Rhynie, Scotland. These specimens are extremely well petrified; therefore many remarkably fine details of structure are known. They are embedded in quartzlike chert by some means that is not fully understood. Whatever the process which brought about such preservation, the plants are standing almost intact in what seems



Rhynia, showing horizontal rhizome with leafless, dichotomously branched upright shoots. The enlarged tips of some of these shoots are the sporangia. (Redrawn from Darrah.)

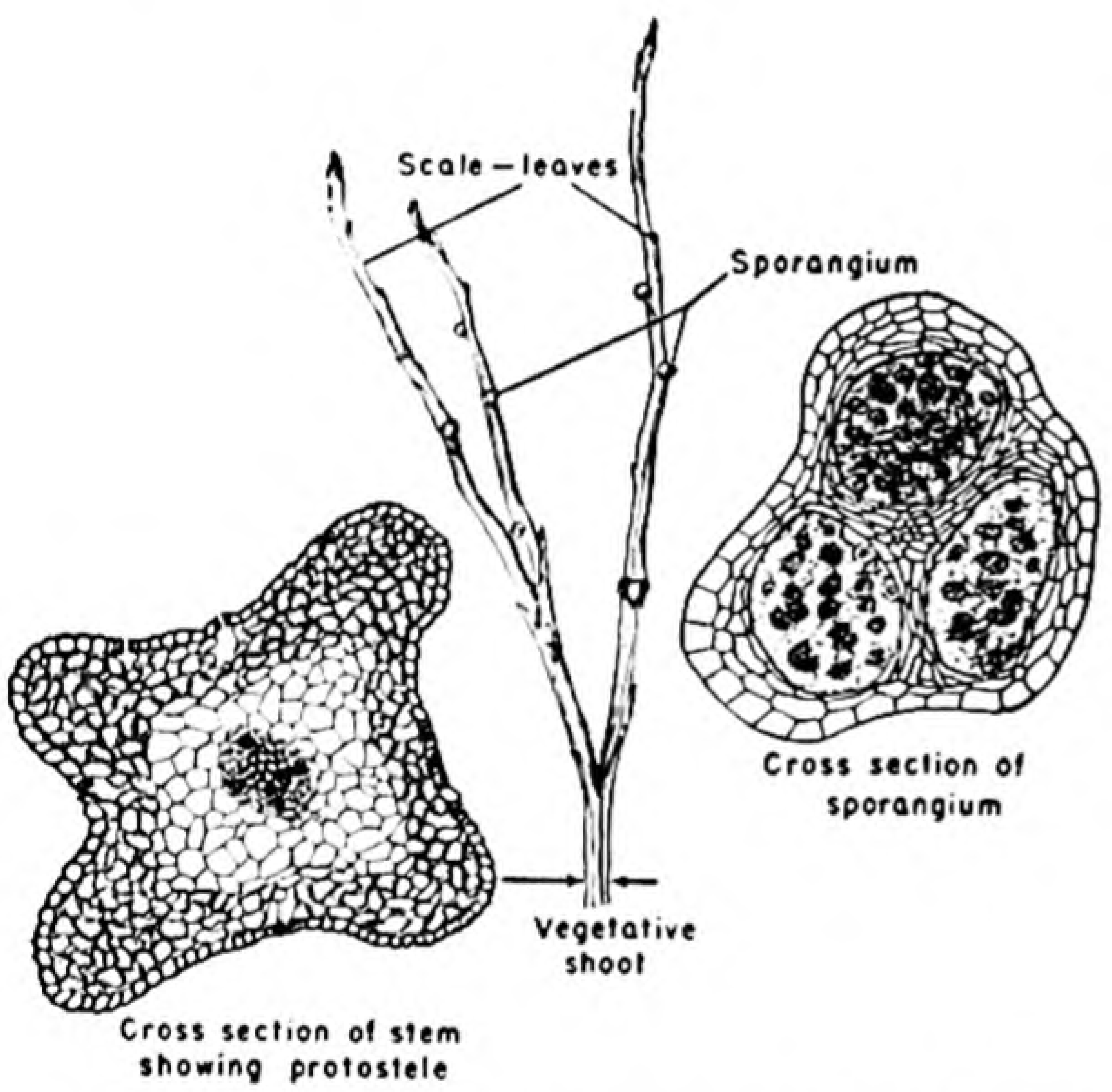
to be swampy or peaty soil. So perfectly are they preserved that the actual cellulose, lignin, and cuticle still remain but little changed. In this fossil bed two species of the genus *Rhynia* have been described. They were much alike. One was about 8 inches tall while the other was a little more than twice as large. Branching was dichotomous. Slightly organized sporangia developed on the extreme tips of at least a part of the stems.

These sporophytes had neither roots nor leaves. Instead, they were little more than stems that grew partly underground and partly in air. Cross sections show them to be simple in both their internal and external structure.

The outermost layer of cells was an epidermis with stomata. Within this was a thick cortex containing extensive intercellular spaces. In all probability this was the photosynthetic tissue of the plant.

Occupying the very center was a narrow strand of xylem composed entirely of tracheids. Completely surrounding it was a zone of phloem cells. This arrangement of parts is called a *protostele* (*protos*, first or primitive) because it seems to be the earliest form to appear in the evolution of vascular plants. All known Psilopsida, ancient and modern, have this type. In addition, it is to be found in a considerable number of representatives of others of the less specialized divisions of the vascular plants. In other words, the protostele seems to be just what its name implies, the most primitive stele.

Psilotum. *Rhynia*, the genus just described, is only one of several known ancient Psilopsida. Others will be described in discussions of the



Psilotum. (*Left*) The cross section shows cortex, endodermis, and chloroplast in its outer layers; and epidermis with stomata. (*Center*) Twig showing dichotomous branching, scale leaves, and three-lobed sporangia. (Redrawn from Coulter.) (*Right*) Section through sporangium showing sporogenous tissue almost ready to produce spores. (Sections drawn from prepared slides.)

probable origins of the various related plant divisions. Here, however, it is more profitable to examine *Psilotum*, one of the living genera, and to compare it with its fossil prototype. This is a genus which occurs in tropical and subtropical regions around the earth. In the United States it is to be found only in South Carolina, Georgia, and Florida.

Aside from the fact that it is much larger, the sporophyte of *Psilotum* is very similar to that of *Rhynia*. It is a dichotomously branched shrub which often attaches itself to the rough trunks of palms, tree ferns, and similar plants. Less frequently it grows among rocks, either taking an upright position or reclining against any available support. Like *Rhynia*, it has no true roots, its subterranean parts taking the form of rhizomes clothed with root-hair-like rhizoids. These, as well as the aerial stems, frequently fork into two branches, some of which become negatively geotropic, growing upward into the air as the aerial shoots.

Comparison of the internal structure of these two kinds of plants makes the similarities of these genera still more impressive. The description given above of the cross section of the stem of *Rhynia* is almost entirely accurate when applied to a similar section through that of *Psilotum*. In one respect, however, *Psilotum* has become somewhat changed: it has a typical endodermis.

In two other ways also the modern *Psilotum* has made some progress beyond its ancient relative. It has large, three-lobed, well-organized sporangia in contrast with the very simple ones of *Rhynia*. It also has leaves on the aerial shoots. They are only poorly developed scales, it is true, but *Rhynia* had none.

No fossils of the gametophyte of Devonian Psilopsida have been found. For this reason the haploid generation of present-day members of this group is very important in gaining an understanding of the total life history. It would not be a justifiable assumption that the gametophytes of living forms are identical with those that grew hundreds of millions of years ago, but they give much information that is valuable in attempting to piece together the relationships of this group.

The gametophytes of *Psilotum* are small and tuberlike. They are monoecious, the archegonia being embedded and the antheridia superficial. The sperms are coiled and have numerous flagella, somewhat reminding one of the swimming cells of *Oedogonium* and its nearest relatives.

Fertilization takes place much as in the bryophytes. The young sporophyte, however, depends on the gametophyte for nourishment for a short time only. Soon it develops rhizomes that extend out into the soil, and aerial shoots that carry on photosynthesis. From this time onward the sporophyte is entirely independent of the gametophyte.

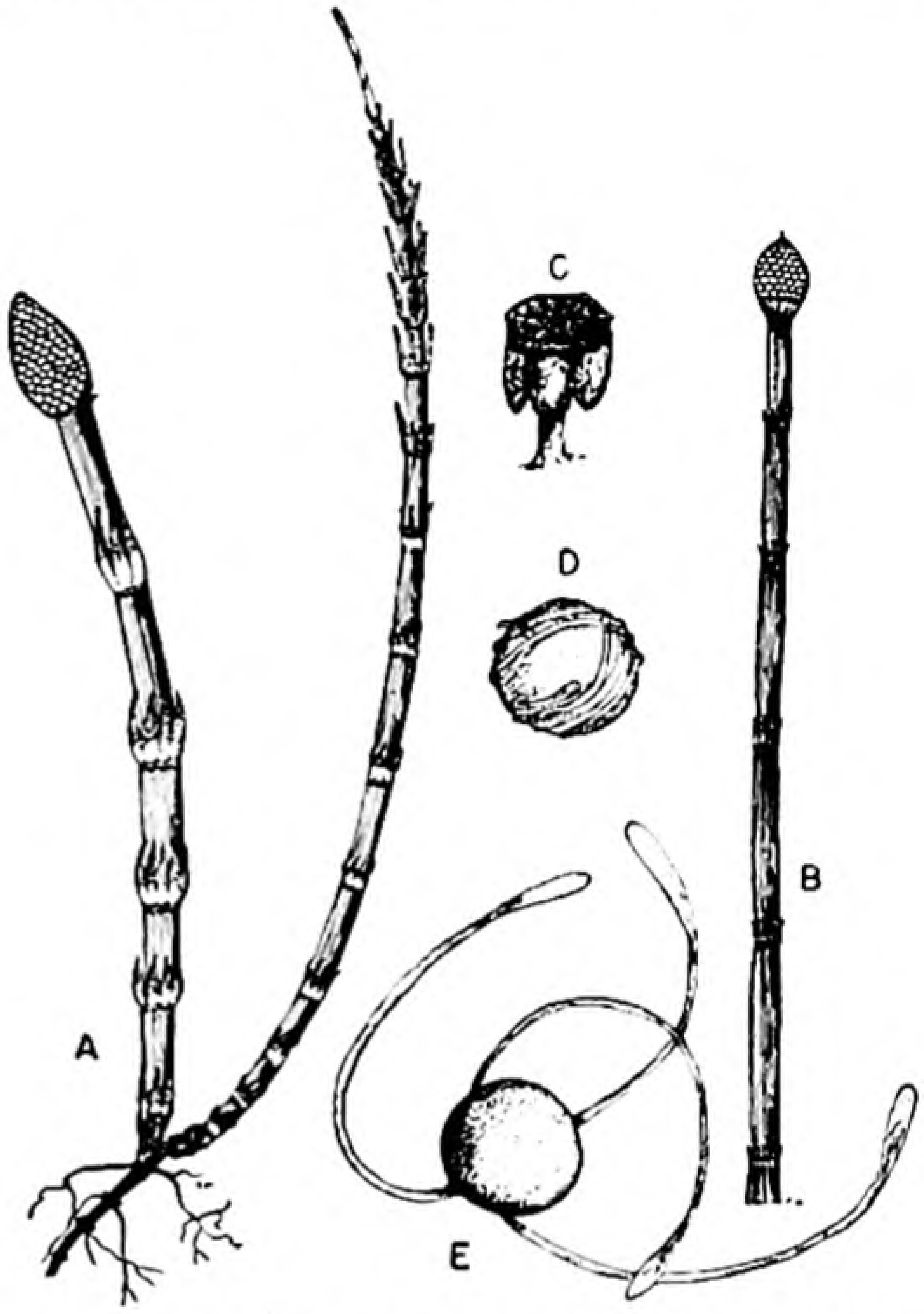
Tmesipteris is the only other known living genus of Psilopsida, and its single species is restricted to the warmer parts of the Eastern Hemisphere. Presumably there has been relatively little change during a period of more than 333 million years in the particular strain of plants to which *Psilotum* and *Tmesipteris* belong. The few living species that persist may therefore properly be called, "living fossils." Though there are many evidences that other groups of modern plants have undergone great changes during this time it is clear that they were originally derived from the widespread ancient stocks of *Psilopsida*.

SPHENOPSIDA

This group of peculiar plants has persisted down through the ages for some hundreds of millions of years. At one time in the earth's history, species belonging to this division of the plant kingdom were important elements in the forests of the time. At present, however, there are only a few score of living forms and they are all included in the one genus, *Equisetum*.

Equisetum. The various species of this genus are scattered over the earth, in all climates from the arctic regions to the tropics and in all the major land areas except Australia. A harsh, abrasive quality, due to the deposits of silica in the epidermis, caused these plants for centuries to be used for many of the purposes now served by steel wool and pumicelike powders, and gave the group the common name, "scouring rush." Some imagined resemblance of the bushy stems of certain species has caused them to be called "horsetails." In fact, the technical name of the genus, *Equisetum* (*equus*, horse; *seta*, a bristle), is the Latin common name for these plants. The sporophyte consists of a system of definitely jointed rhizomes which grow at various depths in the soil. At the joints or nodes there are numerous small, fibrous roots.

Upright shoots grow from the rhizomes, forming simple or branched aerial stems which have no foliage leaves. The photosynthetic function is accomplished by the green stems, and the leaves are represented by a whorl of brownish scales at each node. Some tropical species grow to a height of 25 or 30 ft. but in order to reach this height they must be supported by other plants because their stems, having no secondary thickening, seldom have a diameter of as much as an inch. Those most often met in the United States are from a few inches to a few feet tall.



Equisetum. (A) *E. arvense*, the common horsetail, showing temporary cone-bearing shoot at left and young, branching green shoot at right. Below is a short piece of rhizome with roots at nodes. (B) *E. hiemale*, showing unbranched stem with whorls of rudimentary leaves at nodes, and cone at upper end of stem. Note that all these stems have numerous longitudinal ridges. (C) Sporangiophore showing base of stalk surrounded by sporangia. (D) Spore with moist elaters. (E) Spore with dry, extended elaters.

The spores are borne in characteristic conelike structures. In many species these terminate the ordinary green vegetative shoots. A well-known example is that of the common scouring rush,

Equisetum hiemale, widely distributed in swampy places and in the ballast of railroads.

Equisetum arvense is another species that is very common both in Europe and North America. Its rhizomes give rise to two kinds of aerial branches. One of these does not have chlorophyll but bears a cone. This shoot comes up early in the spring, grows to a height of from a few inches to a foot, sheds its crop of spores and dies, the whole process requiring only two or three weeks under ordinary conditions.

The chlorophyll-bearing vegetative shoot appears at about the same time or a little later. It has a straight, erect main axis from which whorls of more slender branches arise at all nodes except the lowest. This part lives through the growing season, and the excess food produced is stored in the rhizomes and is used by the fertile shoots of the following year.

In all species the spore-bearing cone is composed of a number of polygonal *sporangiophores* arranged spirally around an axis. Each sporangiophore is attached by a stalk arising from its center like the handle of an umbrella. From its edges, pocketlike sporangia extend inward toward the axis of the cone.

The spores are all alike in size. By a peculiar spiral splitting of the outer wall, four thin appendages are formed, all of which remain attached at one point. These appendages, called *elaters*, are composed of two layers of material. The inner is of a waxy substance that does not imbibe water, while the outer one takes up moisture and swells with remarkable speed. For this reason, the elaters wrap firmly around the spore as long as they are moist, and extend outward when they become dry. When observed with the microscope they can be seen to straighten as they dry and to curl about the spore even when so little moisture as that from the human breath reaches them. In nature these appendages are very active and often become entangled when the sporangium opens. As a result, the spores are held together in small masses.

It has been suggested that this type of grouping may facilitate fertilization by causing the gametophytes to grow in small colonies since some of them tend to produce archegonia and others antheridia.

The haploid generation of these and various others of the vascular plants is commonly called a prothallium. The prothallium of *Equisetum* takes the form of a flat green body somewhat like that of a liverwort. Its margin is usually much lobed and very irregular. The antheridia form on its surface and the venters of the archegonia are somewhat sunken into its tissue. The sperms are much like those of *Psilotum*.

Ancient Sphenopsida. During the Devonian period there was a small group of plants represented by the two genera, *Hyenia* and *Calamophyton*. These plants had jointed stems, leafy branches, and sporangiophores somewhat like those of *Equisetum*. On the other hand, the branching was dichotomous. This, and a few other characteristics strongly suggest the Psilopsida. In fact, some paleobotanists think that these genera should be classed with that division while others place them in the Sphenopsida. However they may be classified, they seem to form a connecting link between the two divisions. In other words, their structure gives a basis for the idea that they arose out of Psilopsidian stock and that they were forerunners of the Sphenopsida.

The typical and undoubted Sphenopsida first appeared at the very beginning of the Mississippian Period. This division of the plant kingdom gradually reached the peak of its importance during the Pennsylvanian Period at which time there were

Annularia, a small branch of *Calamites* with its leaf whorls.

large numbers of species ranging in size up to that of large trees. Some of these, belonging to the genus, *Calamites*, had much the form of greatly exaggerated horsetails, and were from 40 to 50 ft. tall. A cambium produced considerable amounts of secondary xylem which gave strength to the upright trunks and to their larger branches.

Like their small present-day relatives, these trees had hollow stems with numerous longitudinal ridges on the surface, and their nodes were definite joints. On the smaller twigs were whorls of well-organized leaves that were almost certainly capable of carrying on photosynthesis. These branchlets with their leaves were originally supposed to be a different small plant called *Annularia*.

One of the amazing features of these great jointed trees was the fact that they grew up from gigantic horizontal rhizomes which increased by secondary thickening until they were a foot or more in diameter. At each of the nodes of the rhizomes and lower trunk numerous roots were produced.

LYCOPSIDA

Modern members of this ancient division of plants are often called "club mosses." This name is given them because in many of the species the spores are borne in long, slender cones having a clublike appearance. In addition, the sporophytes often have a strong superficial resemblance to moss gametophytes.

These sporophytes remind one of certain of the ancient Psilopsida. In many species there are extensive rhizomes with aerial shoots that bear small leaves but these underground stems are well supplied with roots. The leaf of the various lycopods is peculiar in that it is a spur of tissue growing out from the stem. A vascular bundle (vein) extends throughout its length, usually without branching. In all respects this simple type of leaf, called a *microphyll*, contrasts with that which is characteristic of the ferns.

There are two rather distinct classes of living Lycopsida. One of these has only one kind of spore, that is, it is *homosporous* (*homos*, similar); the other has two widely differing kinds, a condition that is called *heterospory* (*heteros*, other). The living homosporous forms are limited to two genera. One of these is the genus *Lycopodium* of moist temperate and, especially, tropical climates, and the other is a single species of *Phylloglossum* which is found only in the region of Australia and New Zealand. All the heterosporous species belong to the genus *Selaginella*.

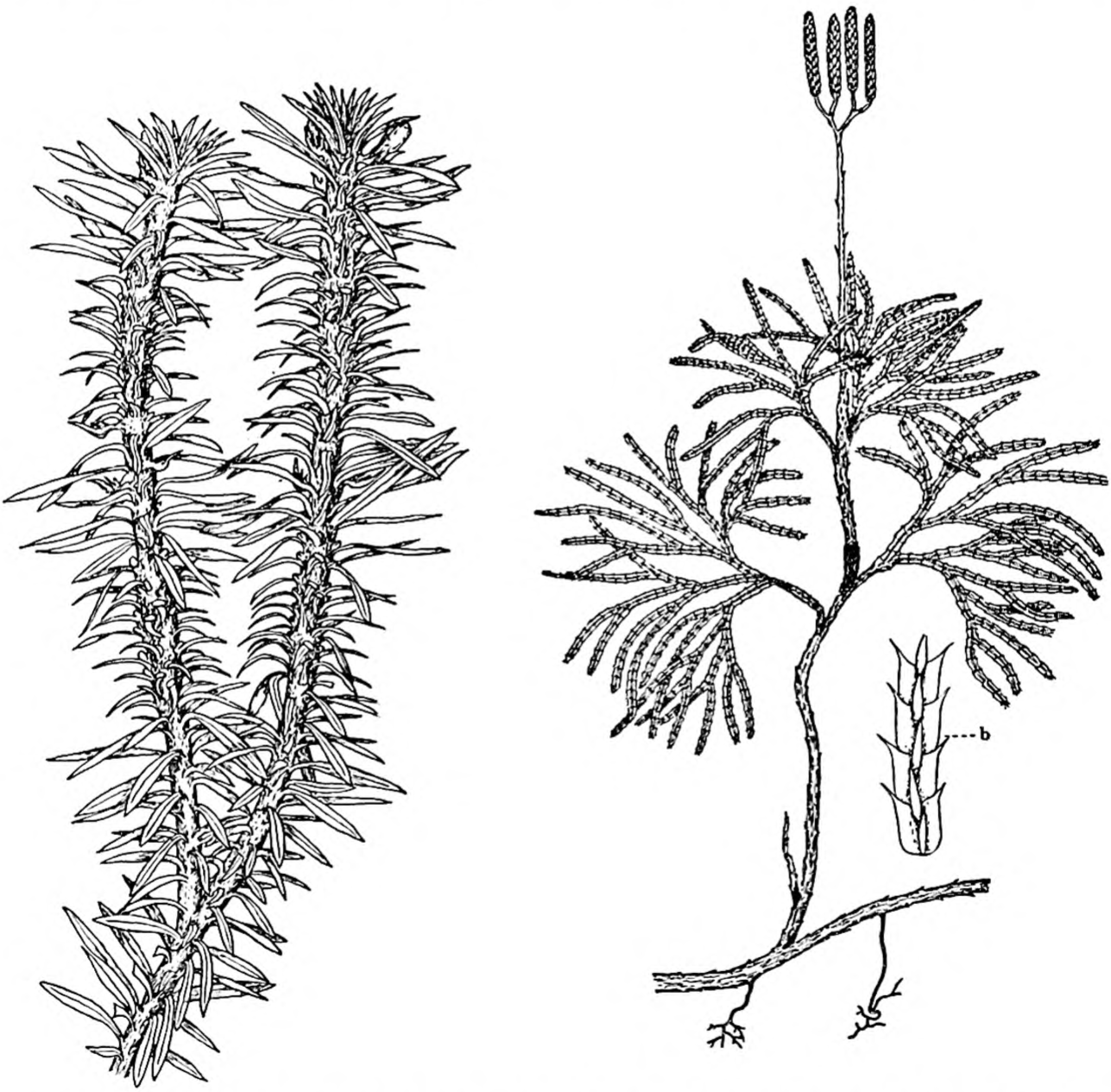
Lycopodium. The different species of *Lycopodium* take various forms. Some have erect aerial stems attached to horizontal rhizomes or runners, while others have rhizomes so short that they may be overlooked. In many species almost the whole plant is prostrate on the ground or reclining on other plants. The stems may be simple or variously branched. The leaves of some are thin, flat, and slender while those of others are short and scalelike.

Tuberous gametophyte of *Lycopodium*, with young sporophyte with roots and shoot attached.

One important characteristic of the stems of *Lycopodium* is the nature of the stele. Cross sections show it to be a protostele much like that of a root, although the xylem often forms more complicated patterns than that in roots.

Some species produce their spores in specialized cones which are made up of reduced, scalelike leaves; in others the sporangia are attached near the bases of ordinary foliage leaves. All species are homosporous. The spores are so abundant that they were formerly collected in great quantities and used by pharmacists for pill coatings. Because of their oily nature, they were used in the past to produce special lighting effects in theaters. When blown from a nozzle, like dust from a dust gun, they can be lighted and burned like gas.

Although the spores are produced in great numbers, relatively few of them ever become effective in reproduction. In some species, the gametophytes are small and green and comparatively short lived, completing their development in a few months; in

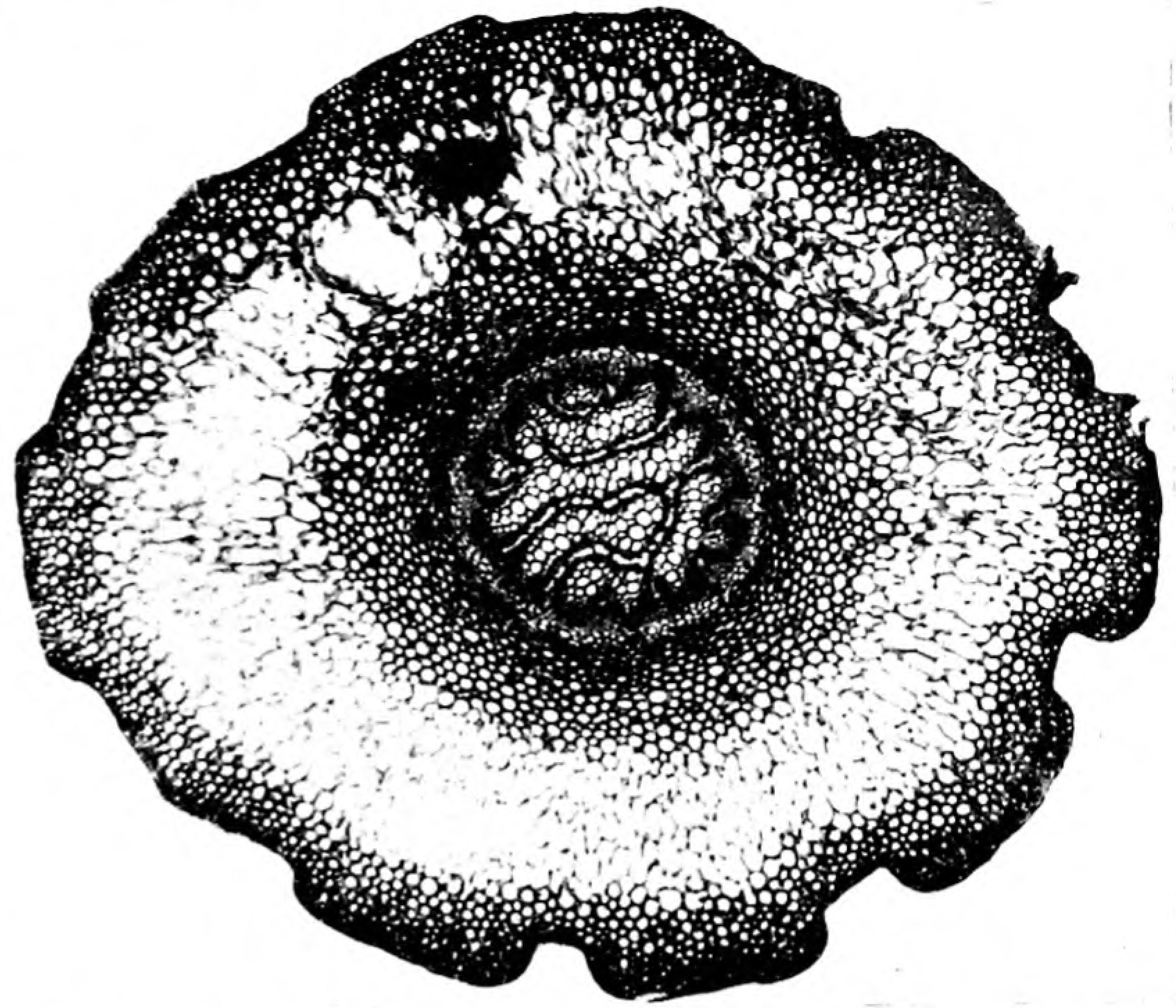


Lycopodium. (*Left*) *L. lucidulum*, showing sporangia in axils of foliage leaves. (*Right*) *L. complanatum*, showing well organized cones of sporophylls at upper ends of specialized branches. Note dichotomous branching of both stems and roots. (Courtesy, Mottier: "College Textbook of Botany," Philadelphia, The Blakiston Company.)

others, they grow underground, developing into larger, tuberlike structures which have no chlorophyll. This latter type may require several years to complete its part of the life cycle. Both kinds have associated with them a mycorrhizal fungus which is apparently helpful to them in securing food.

The sex organs and gametes, the details of fertilization, and the formation of the young embryo have their own peculiar characteristics, but the general story is that of a swimming, terminally biflagellate sperm uniting with an egg in an archegonium and the resulting zygote developing into a rooted, leafy sporophyte.

In addition to the sexual method some of the species have a very efficient vegetative form of reproduction by means of specialized buds, called *gemmae*. These grow along the stems of the sporophyte and later fall to the ground and take root.



Cross section of stem of *Lycopodium*, showing sclerenchyma in both outer and inner cortex. In the stele the largest cells are tracheids of the xylem. A zone of phloem can be seen around xylem, but strands of phloem also extend in narrow strips between layers of xylem.

Selaginella. The species of *Selaginella* are more numerous than those of *Lycopodium* but the individual plants are much smaller, and on the whole this genus is by far the less prominent of the two.

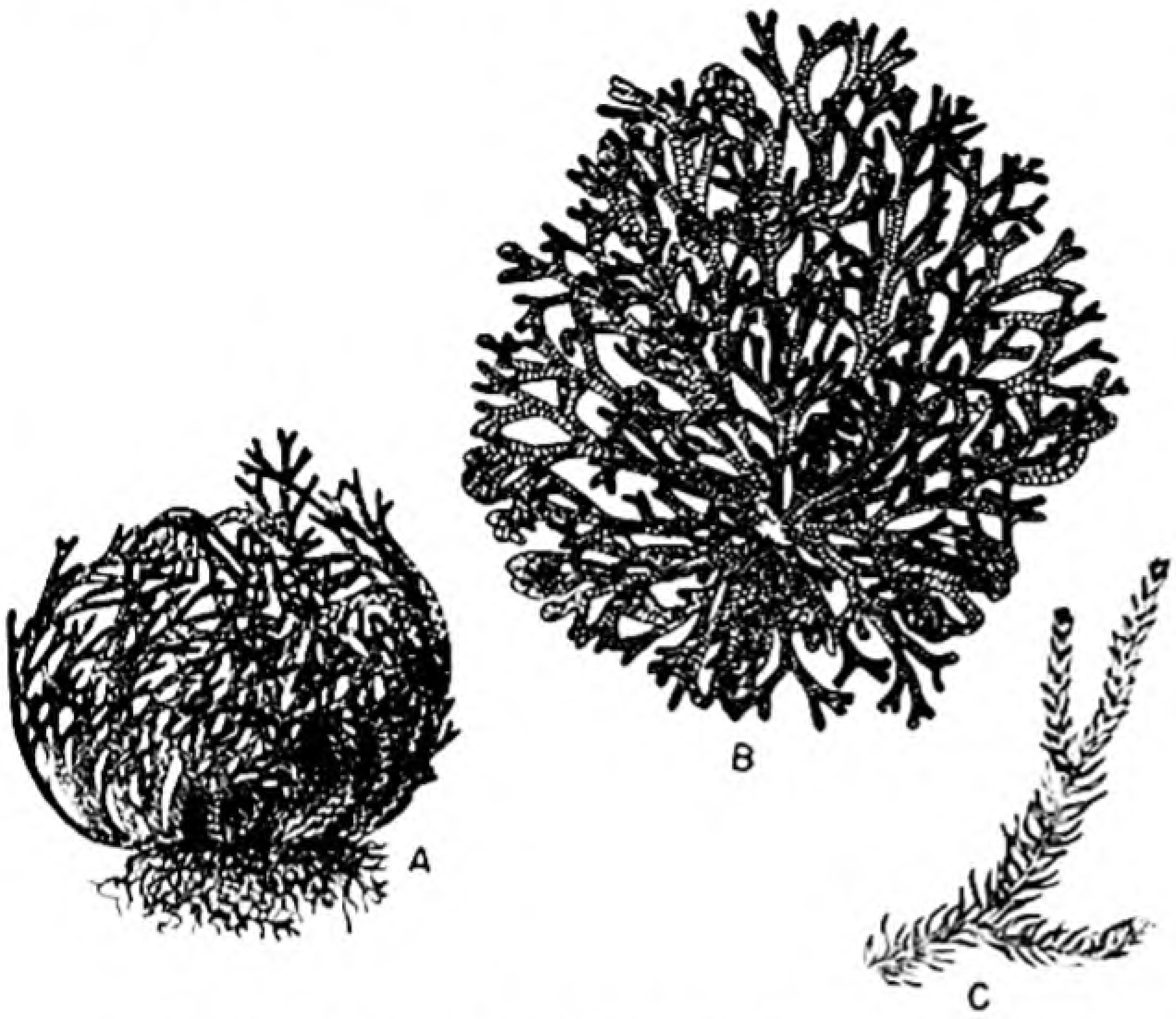
In the different species the sporophyte appears in about the same variety of forms as does that of *Lycopodium*, but in miniature. There are, however, a number of significant differences in the details of the life history. The various species of *Selaginella* are adjusted to a large number of climatic conditions. Some live in the tropical rain forests, some in swamps and moist woods, and others in dry places. The last sometimes grow under semiarid and desert conditions, and the dry, gray inrolled plant may remain for months apparently dead, only to unroll and turn green within a few minutes after moisture is applied. The "resurrection plant" sold in curio shops is *Selaginella leptophylla*, a species from arid, rocky places in the Southwest, and S. *densa* is an important ground cover in the drier parts of the West.

In most species of this group the stem has a protostele. A few, however, are more highly specialized. Some have a peculiar type of siphonostele, and one shows a small amount of secondary thickening.

The sporangia are borne singly in the axils of specialized leaves, technically known as *sporophylls*, and these are arranged in four rows in a cone or *strobilus*, which usually differs little in appearance from a vegetative shoot. The spores are of two kinds, *microspores* and *megaspores* (*mikros*, small; *megas*, great) and the sporophylls which bear them are known as *microsporophylls* and *megasporophylls*. Each strobilus usually has both kinds.

A microsporangium contains several hundred microspores, but the megasporangium usually produces only four megaspores, these coming from one mother-cell and constituting a typical tetrad. Both kinds of spores may fall to the ground, the entire strobilus may fall off, or the microspores may fall into the axils of the megasporophylls where both they and the megaspores germinate.

When microspores germinate, they produce *male gametophytes* only; *megaspores* develop into *female gametophytes*. The entire development of the male gametophyte takes place inside the wall of the



Selaginella leptophylla (A) In dry condition. (B) A few minutes after being placed in water. (C) Small shoot of *Selaginella* with two cones.

microspore, and the female gametophyte protrudes only slightly from the cavity of the megaspore. The germination of the spores in forming the gametophytes may begin before the spores leave the sporangia. The gametophytes are short-lived, since neither has chlorophyll and they depend entirely upon the food stored in the spores.

The sperms swim by means of a pair of flagella in a film of moisture provided by rain or dew, and fertilization is followed quickly by the formation of the young sporophyte.

When the development of the gametophytes takes place in the axils of the megasporophylls where the microspores have fallen, the young sporophytes may remain there until their primary roots and first few leaves have been formed, when they fall to the ground and continue their growth. These embryo plants protruding from the axils of the sporophylls, demonstrate the fact that this plant closely approaches the production of seeds. Seeds, it should be explained, are embryo sporophytes surrounded by a protective cover and having a longer or shorter dormant period.

Isoetes. The peculiar little plants belonging to this genus are so different in appearance from any others to which they might be related that their position in the plant kingdom has long been a subject for debate among botanists. Since they have several technical characteristics that suggest the club mosses, they are included here for convenience. These plants grow in water or in wet places and are mostly limited to the cooler climates of the Northern Hemisphere.

The leaves of the sporophyte have very much the appearance of the stems of many of the sedges and rushes usually found in the same habitats. The plant consists of a very short, thick stem that gives rise to numerous hollow cylindrical leaves and to short dichotomously branched roots. Superficially, it has the appearance of a small lily with a poorly organized bulb.

The stem has a very complex anatomy the primary aspects of which are obscured by a peculiar secondary thickening. The plant is a long-lived perennial. The tissues produced on the outside of the

Selaginella densa, growing over rock surface. At right, sufficient soil has accumulated to permit a grass plant to become established.

cambium die and decay. The increase in size, therefore, is not very great. The leaf has a single vascular bundle and four longitudinal, septate air canals.

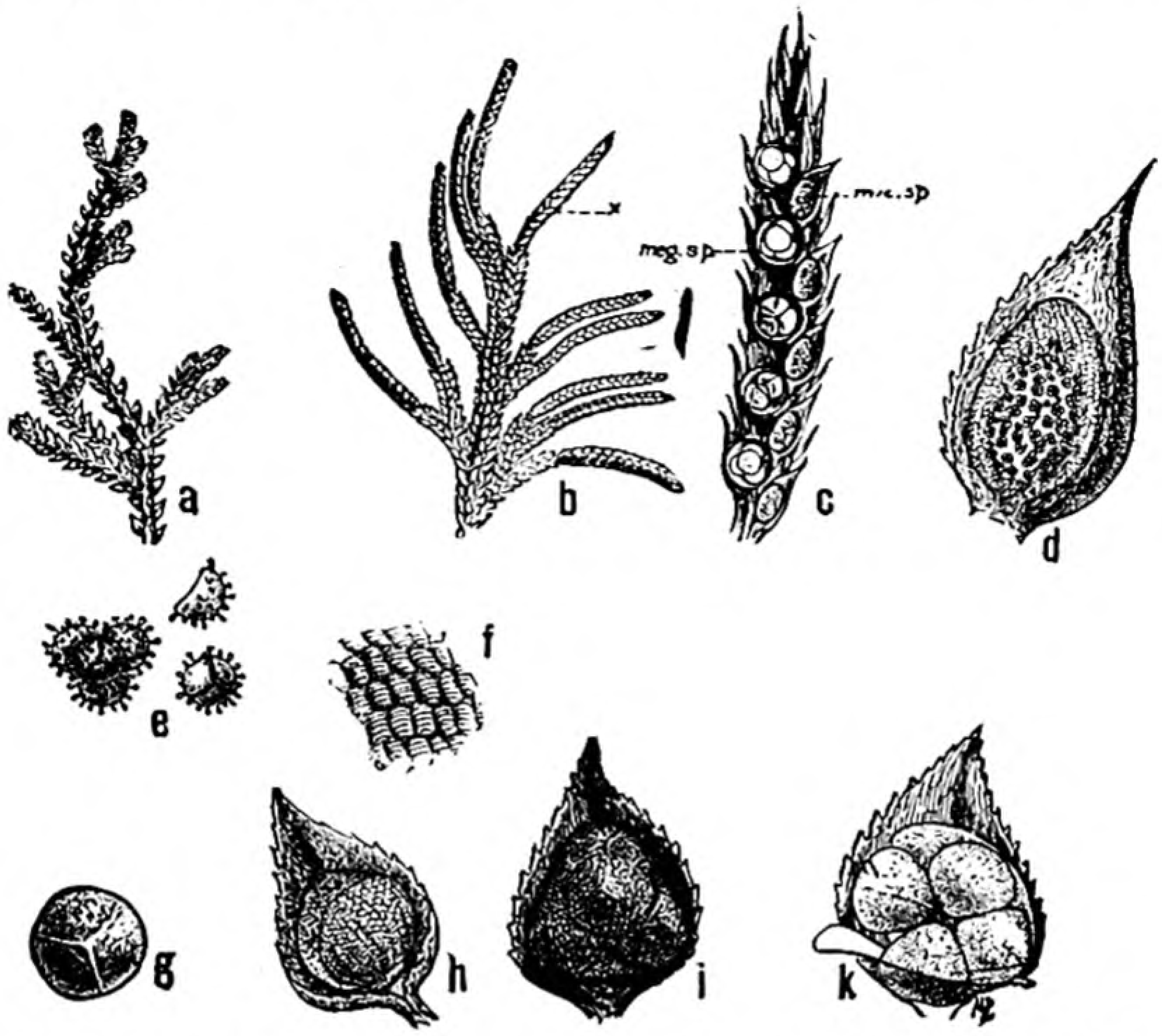
Either a microsporangium or a megasporangium forms at the base of each leaf. A megasporangium may contain as many as 100 spores, and some of the microsporangia are said to produce more than a million. Both kinds remain in the sporangium until the dead sporophylls disintegrate during the winter.

As in the other heterosporous species which have been described, the gametophytes are so small that their entire development takes place inside the spore wall. Little is known about fertilization, but it is apparently much the same as in *Selaginella*.

Ancient Lycopsida. Most botanists are inclined to suppose that the Lycopsida arose from the Psilopsida.

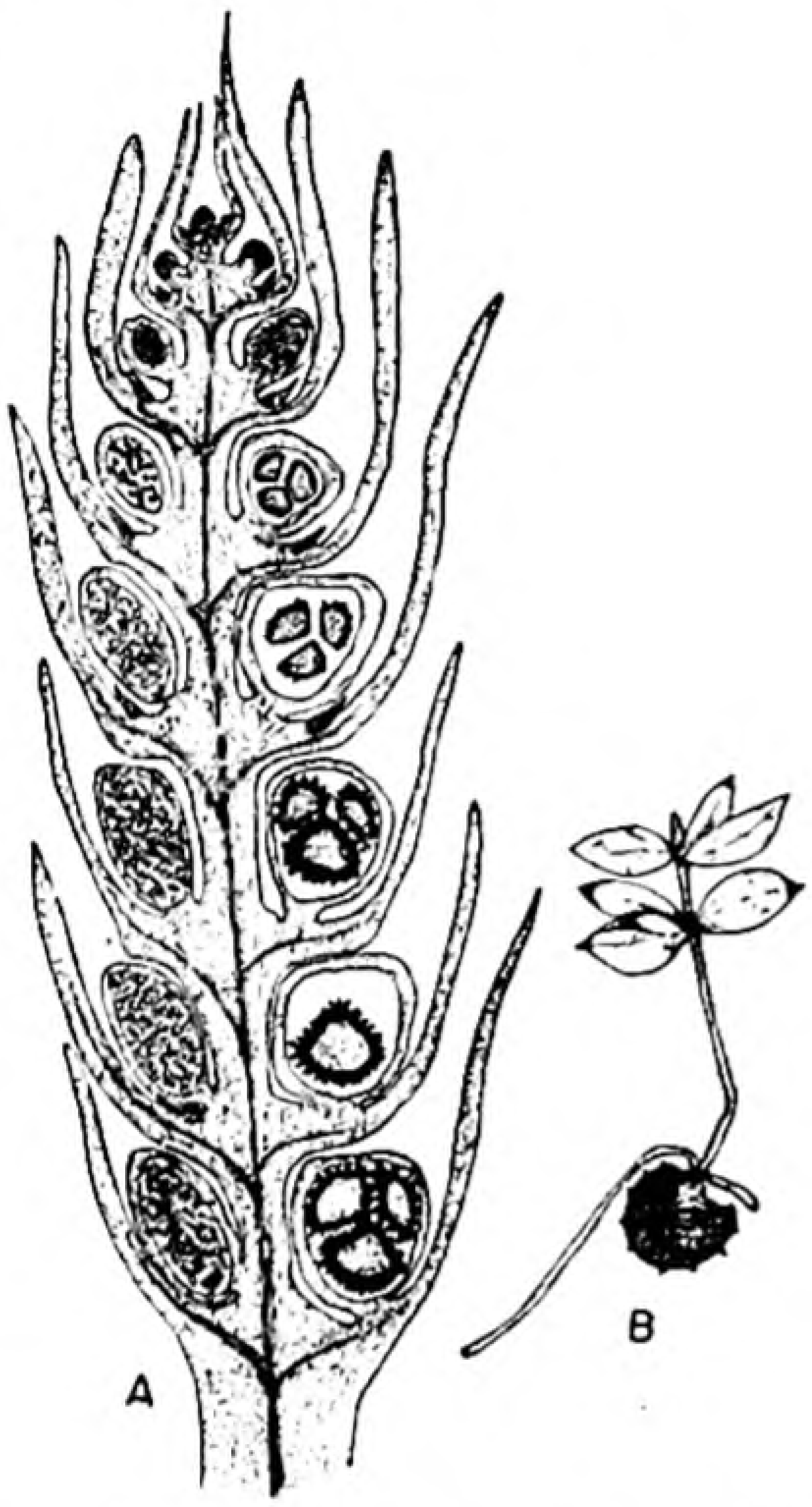
Asteroxylon. One of the most enlightening forms is *Asteroxylon*. This plant is known from the Devonian period in two localities in Europe—one in Scotland and the other in Germany. It was much like *Rhynia* but was distinct from that genus in that it had spurlike leaves (*microphylls*) on its aerial stems. These leaves were not more than 5 mm. long. There were stomata in the epidermis; therefore clearly they must have been photosynthetic organs. Sporangia have not been found attached, but detached *Rhynia*-like ones are thought to belong to these plants. Obviously *Asteroxylon* occupied a somewhat intermediate position between *Rhynia* and *Lycopodium*.

Much of the coal of the Carboniferous period was produced by great swamp forests whose trees were largely giant club mosses and horsetails. Var-



Selaginella Martensii. (a) Vegetative branch. (b) Portion of the stem, bearing cones (x). (c) Longitudinal section of a cone, showing microsporangia (mic. sp.) in the axils of microsporophylls, and megasporangia in the axils of megasporophylls. (d) Microsporangium with microsporophyll. (e) Microspores. (f) Portion of wall of sporangium, greatly magnified. (g) Megaspore. (h) Microsporangium opened, and most of the microspores scattered; (i) Megasporangium, with megasporophyll. (k) Same, opened, showing the four megaspores. (From Gager: "General Botany.")

ious ones had an active cambium which added much secondary wood to their great trunks. Evidence is strong that these forests occupied some areas over extremely long periods of time. When the trees or their parts fell into the water or mud



Selaginella. (A) Strobilus with small microspores, and very large megaspores. (B) Young sporophyte emerging from within female gametophyte enclosed in megaspore wall.

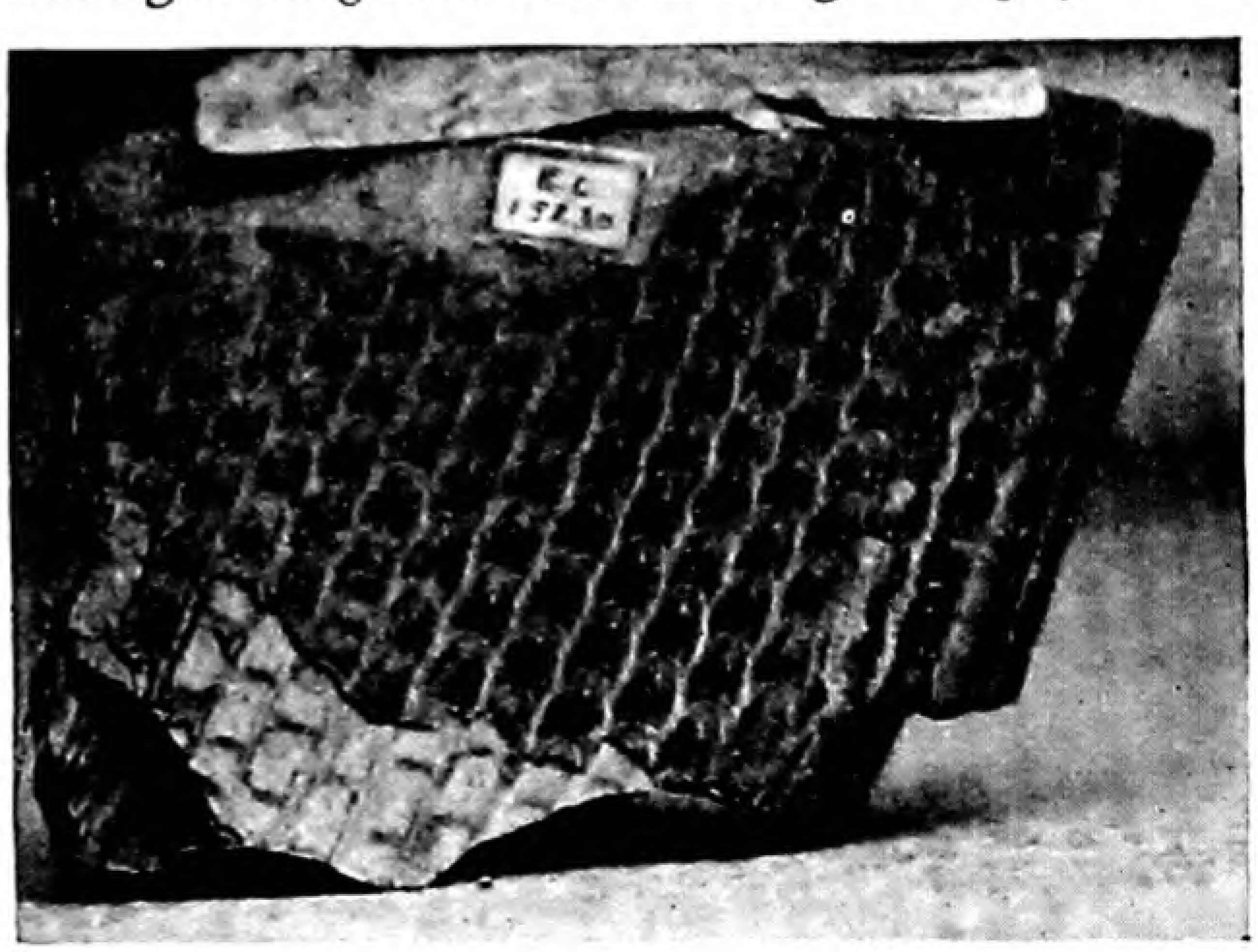
they failed to decay. In many cases such masses of peatlike material became covered with mud. Tremendous weight built up. Pressure through the ages flattened this mass, and infiltration with dissolved minerals cemented it together. The organic minerals, cut off from oxygen, failed to disintegrate. They became coal and the muds changed to shale.

This group reached its highest expression both in size of plant and in number of species during the Mississippian and Pennsylvanian periods. In fact Lycopods of tree size, along with *Calamites*, made up a conspicuous part of the forests of that time. Most important of these tree lycopods were *Lepidodendron* and *Sigillaria* (see pp. 165, 286). Representatives of both genera are known to have grown to a height of 100 ft. or more. The leaves of *Lepidodendron* were attached in spiral lines around the stem, and those of *Sigillaria* were in vertical lines. The two genera can be distinguished by the position of the leaf scars as seen in fossils.

Sporophyte of *Isoetes*, showing leaves and dichotomously branched roots arising from very short stem. Sporangia may be seen as swollen objects at bases of leaves.

Some of these trees may have been homosporous but the majority appear to have been heterosporous and a few are known to have produced a peculiar type of seeds which are quite distinct from those of any modern plants.

As an example, the seed of *Lepidodendron*, called *Lepidocarpon*, was a megasporangium containing a *Selaginella*-like female gametophyte and



Sigillaria. Leaf scars in vertical lines.

largely enclosed by a cup-shaped sporophyll. This acted as an integument which remained slightly open at the end, leaving a sort of micropyle. Nothing is known of the microspores and male gametophytes. As we shall see later, this is very primitive and not quite a true seed in the modern sense.

By the beginning of the Mesozoic Age this entire group of tree forms had died out and only the smaller, more nearly modern types remained to perpetuate the division down to the present time.

The Mississippian and Pennsylvanian Periods, sometimes called collectively, the Carboniferous, were times in which great beds of coal were being formed. Embedded within much of this coal are impressions and actual structures of the plants that entered into its composition. Many of these plants were small, but the largest and therefore most important from the standpoint of the amount of coal produced, were the giant members of the Sphenopsida and Lycopsida. The great Carboniferous coal fields of the present time originated as extensive forests of these primitive trees with their undergrowth.

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Chapter 19

PTEROPSIDA: FILICINEAE—THE FERNS

There is no clearer place in the plant kingdom in which to become thoroughly acquainted with the alternation of generations than in the true ferns. In these plants the sporophyte and gametophyte generations are almost independent of one another. For this reason the two generations contrast sharply.

This division of the plant kingdom has existed from Devonian times to the present (see p. 169). The organization of this chapter is as follows:

How to Recognize Common Ferns
The Sporophyte
The Gametophyte
Fertilization
The Embryo
The Origin and Evolution of the Pteropsida

The division Pteropsida is the culminating division of the plant kingdom. All of the most complex and at the same time the most successful plants of the present day belong to the Pteropsida. These plants are now playing a remarkably important part in controlling the total world of life.

To understand the significance of this statement it must be recognized that every tree in every forest, every grass plant on the Great Plains and, although much less important, every fern, wherever it may be, is a member of this division. This group of plants furnishes by far the greatest part of the food devoured by the myriads of animals, as well as that which nourishes the fungi and bacteria. The roots and rhizomes belonging to members of this division constitute the greatest of all controlling factors that reduce the loss of soil by erosion. At the same time leaves and branches from these plants continually contribute to the fertility of the soil in which their roots grow.

The division Pteropsida is composed of three great classes. They are Filicineae—the ferns; Gymnospermae—seed plants that have no pods or other enclosures around the seeds; and Angiospermae—modern seed plants with enclosed seeds.

So important is each of these classes that they require separate treatment. In this chapter the ferns will be discussed. It should be understood, however, that in popular usage the name fern is often applied to a considerable number of plants that do not belong to the Filicineae. As an example, there are two species of plants that are frequently called "asparagus ferns." They are closely related to the garden asparagus, an angiosperm. Such errors in naming come from the popular idea that any plant of considerable size with finely divided leaves is likely to be a fern. This idea, however, is far from the truth. Many common seed plants have compound or dissected leaves and a considerable number of ferns do not.

How to Recognize Common Ferns. A good field test by which to determine whether a plant under observation is a fern or a seed plant is to examine the young leaves. Those of ferns develop

Tropical fern with broad, strap-shaped leaves.

by unrolling at the tip, forming the so-called "fiddle heads," the basal portion of the leaf being the oldest part. This *circinate vernation*, that is, coiled arrangement of the immature part of the leaves, occurs in all but a few genera of true ferns and in no seed plants except some of the cycads. These will be discussed in the next chapter. In addition, the veinlets in the leaves usually fork into almost equal branches somewhat like the letter Y. In some species the forks unite with their neighbors, producing a peculiar network. Even in these, however, the fernlike branching can be made out. This *dichotomous venation* sets the ferns off from all modern seed plants with the one rare exception of *Ginkgo*, which is described in Chapter 20. Besides the peculiarities of venation and vernation, two other characteristics are often useful in distinguishing ferns from other plants. They are, first, *ramentum*, the chaffy scales which usually clothe the base of the petiole; and second, fruit dots or *sori* on the underside of ordinary foliage leaves or on somewhat specialized leaves or leaflets. In most species the sori are present only at certain times of the year.

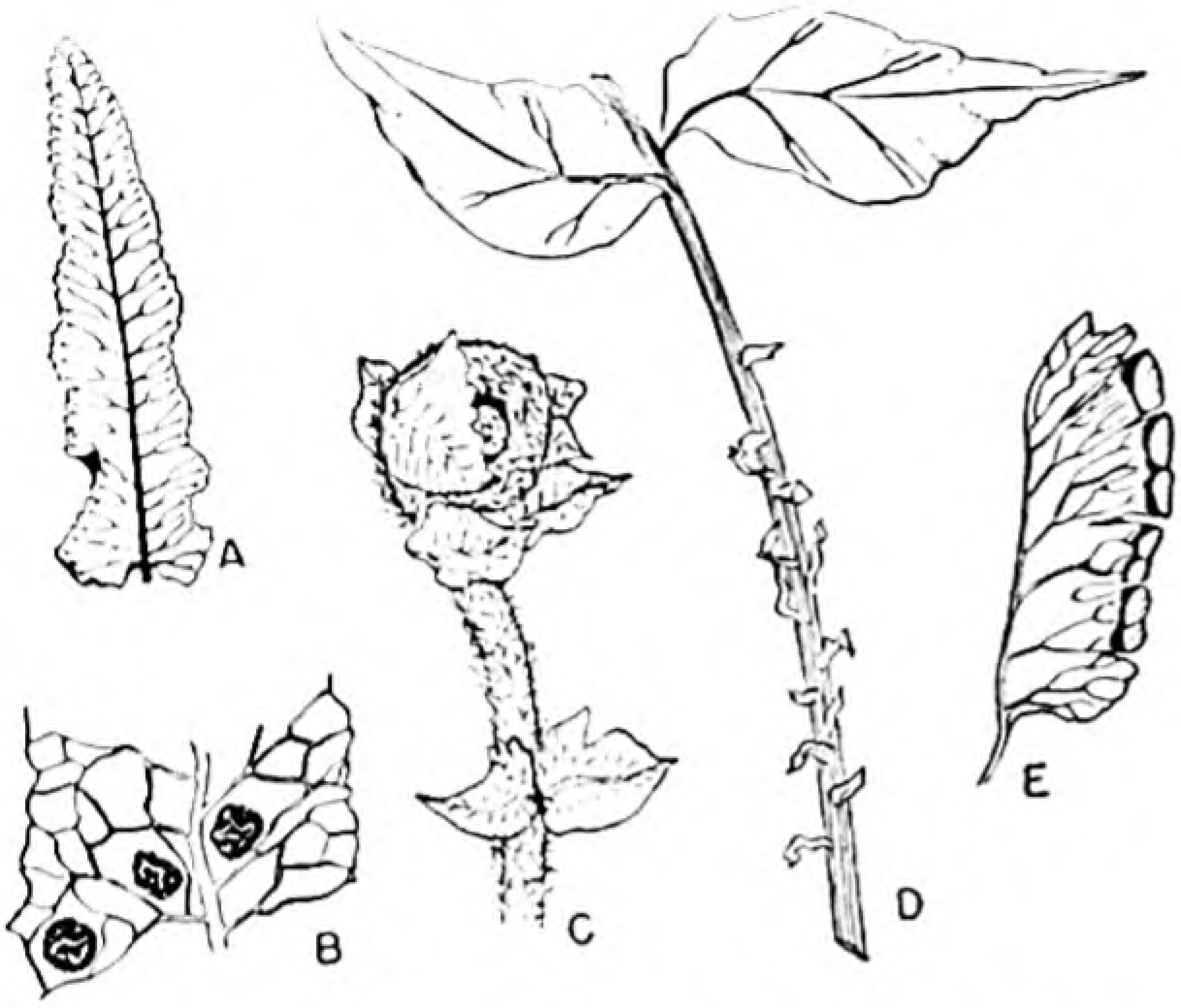
By far the greatest number of ferns live in damp woods, although some are very successful in drier soil in open fields. Others live in very dry, sunny places and even in deserts, where their leaves remain rolled together as if they were dead, except at the time of occasional rainfall. Then they unroll, become green, and growth processes take place normally until the plant again dries up and becomes dormant.

Almost all species are perennial. Those of temperate climates commonly have a horizontal rhizome which lives from year to year, although very few have evergreen leaves. Some of the tropical ferns assume much this same low form but others grow to be trees, the tallest attaining a height of perhaps 80 ft. A considerable number of tropical species are epiphytic, growing far above the ground on the trunks and branches of various kinds of trees, and a few have long aerial vinelike stems.

The Sporophyte. The fern plant of woods, fields, or greenhouse represents the sporophyte generation of the life cycle. In contrast with the sporophyte of the Bryophyta, the fern sporophyte

Circinate vernation of fern leaves.

has roots, stems, and leaves, and a well-developed vascular system. It is permanently independent of the gametophyte as soon as its roots and leaves have been established.



Characteristics of fern leaves. (A) Dichotomous venation. (B) Dichotomous venation with veinlets reuniting into network. Three sori are shown, each with the remains of an indusium. (C) Circinate vernation. (D) Ramentum. (E) Sori, made up of numerous sporangia covered by indusia.

All the major types of steles are represented in the Filicineae. The most primitive and the most ancient is the *protostele* with its central shaft of xylem surrounded by phloem. The *siphonostele* seems to have been derived from it by a failure of a part of the xylem to organize as conductive tissue, resulting in the establishment of a central pith. The reasons why this kind of structure is a mark of advancement over the protostele are obscure, but it is an observed fact that plants with protosteles in their stems are always comparatively primitive.

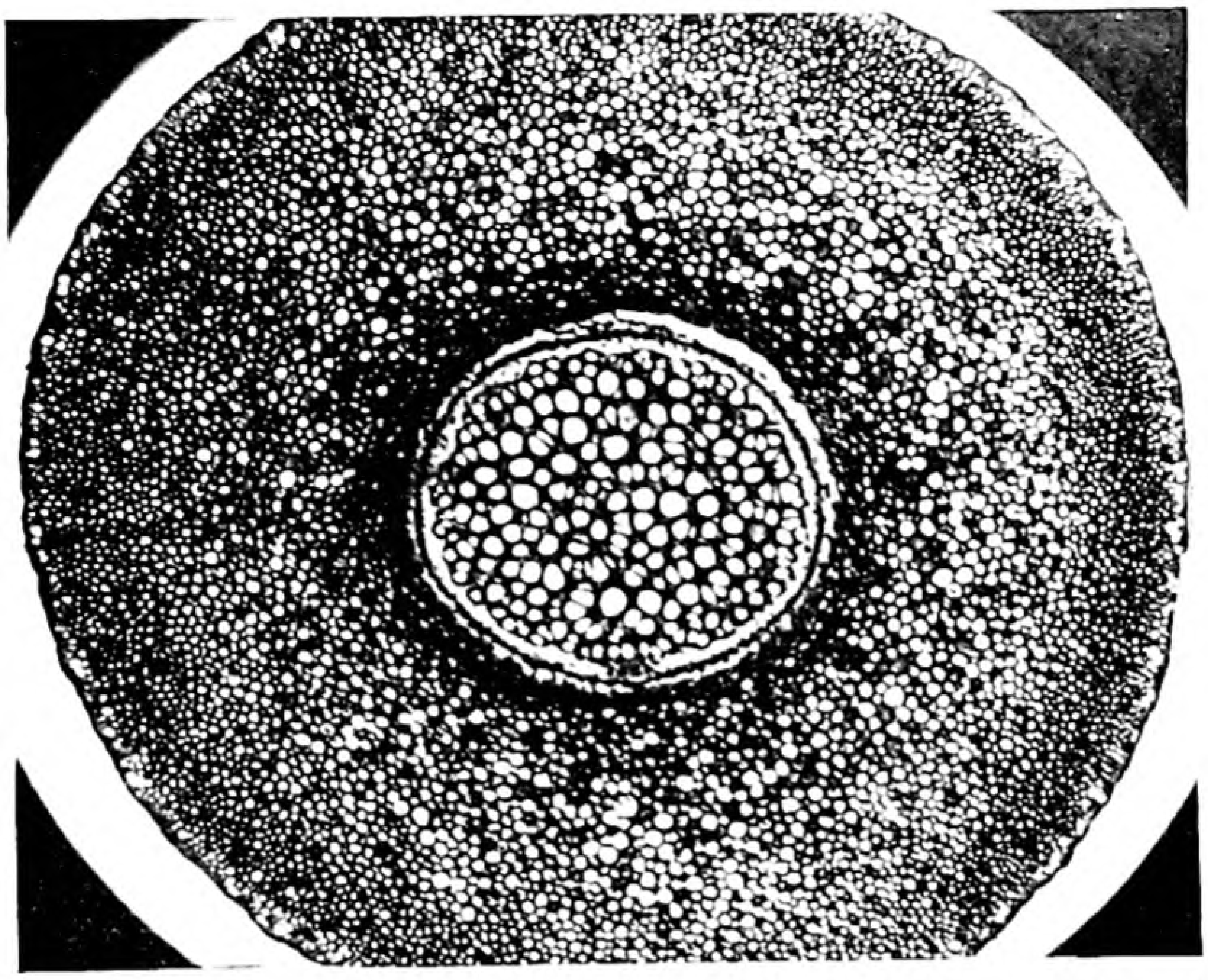
Some siphonosteles, especially of higher plants, have very narrow xylem rays and others have wide ones forming, respectively, the *continuous* and *dissected* types. Those of the dissected type sometimes become greatly disarranged, forming the *scattered stele*.

THE PROTOSTELE. The stems or rhizomes of a considerable number of ferns have a stelar structure very similar to that of the Psilopsida and Lycopsida. The rhizome of some species of the tropical fern, *Gleichenia*, is a good example. Occupying the center of this underground stem is a relatively large shaft of xylem. The greater part of this tissue is composed of thick-walled, woody tracheids. Occupying spaces between them, however, are numerous parenchyma cells that can be recognized by their thin walls. More or less completely surrounding the xylem is a rather irregular layer of phloem and around this is the pericycle. Sometimes the pericycle can be readily recognized as a definite band of rather thick-walled cells and sometimes it is less distinct. It marks the outermost part of the stele. Enveloping it is the cortex.

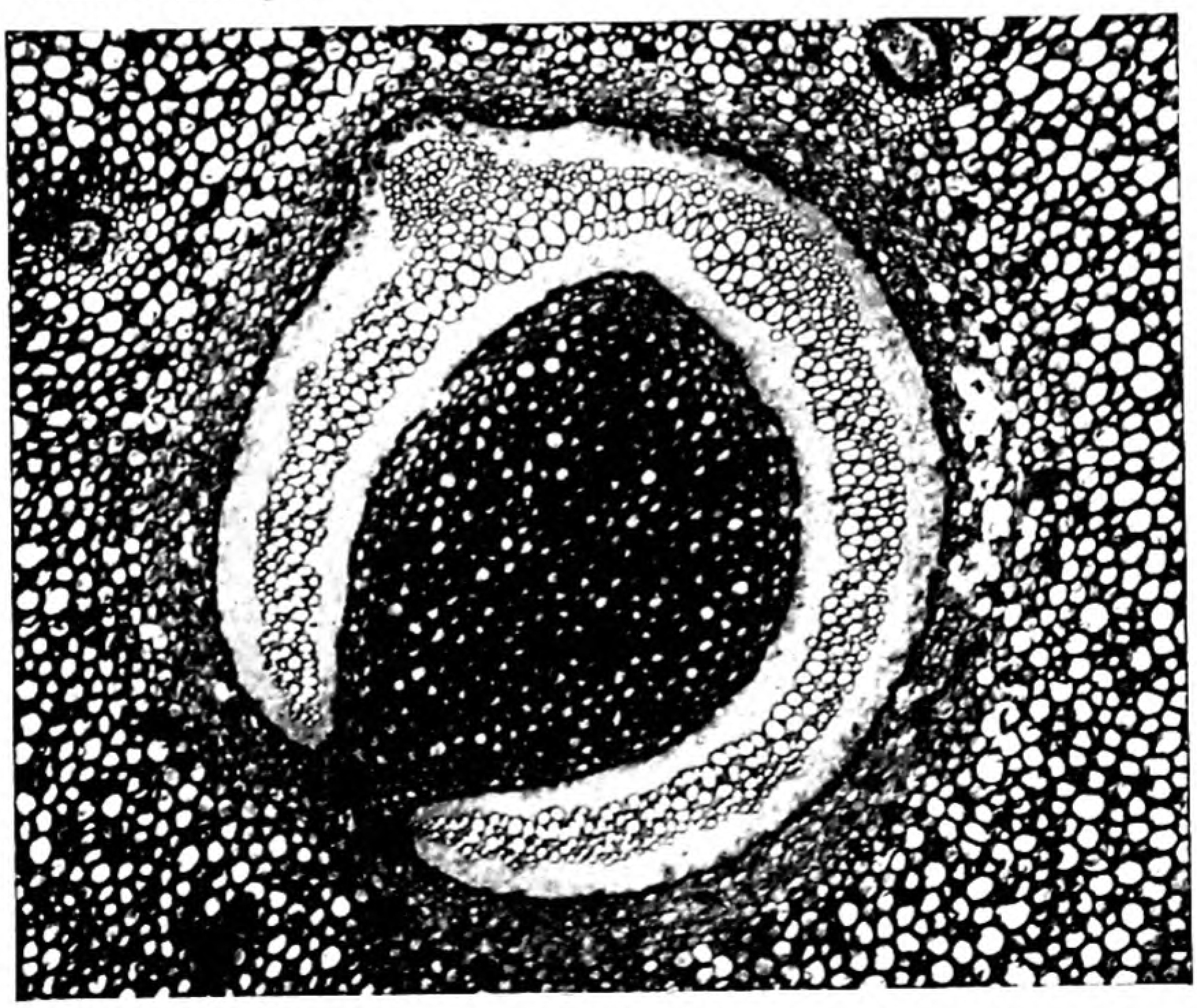
Small spots of vascular tissue which may be seen in the cortex in some sections are the *leaf traces*, extending out from the stele of the stem into the leaves, where they branch and become the veins.

THE SIPHONOSTELE. A simple form of siphonostele occurs in the rhizome of the common maidenhair fern, *Adiantum pedatum*. Cross sections of this underground stem cut between the nodes show a definite ring-shaped stele inside the cortex. The innermost part of the cortex is, as usual, a single layer of somewhat specialized endodermal cells. The outer part of the stele is the pericycle. Then come the phloem and xylem. Cambium is lacking. In the center of this stem there is a considerable amount of central pith. But, surprisingly, there is also another layer of phloem in contact with the inner surface of the xylem. This condition in which

Desert ferns, *Notholaena standleyi*, growing in a pocket of soil in lava bed. Carrizozo, New Mexico.



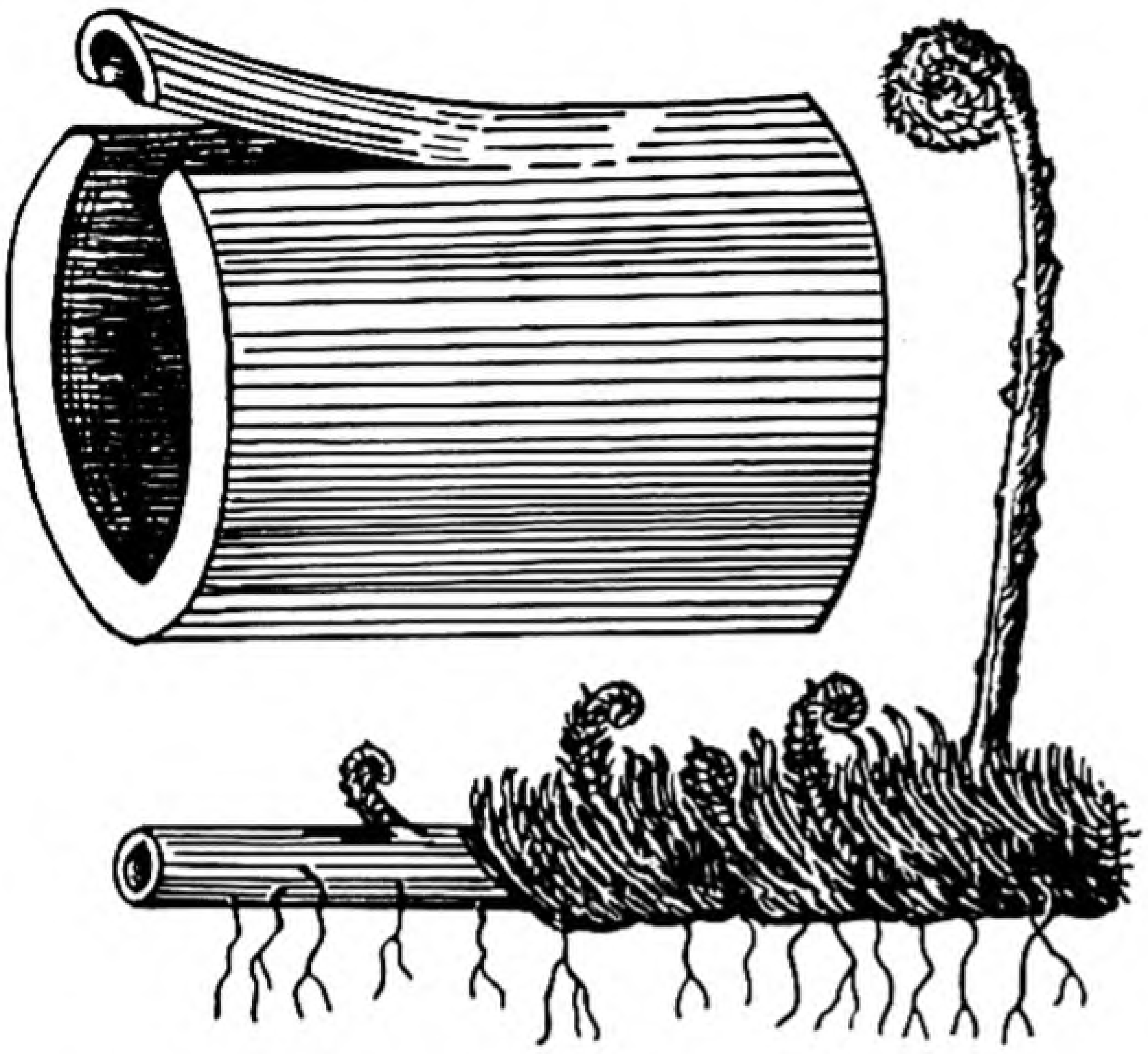
Protostele of *Gleichenia*. Xylem, occupying entire center of stem, is surrounded by phloem. Epidermis and cortex are clearly seen in usual positions.



Siphonostele of *Adiantum*, showing dense central pith almost enclosed by horseshoe-shaped vascular region. Xylem is recognizable by large tracheids. Completely enwrapping the xylem on all sides is phloem. The dark line that separates phloem from cortex and from central pith is endodermis.

The open side of the stele is the leaf gap. Its leaf trace is not shown in photograph, but two other leaf traces can be seen near upper edge.

xylem is covered on both surfaces by phloem is not common, but is known in several plants. Such an arrangement is called an *amphiphloic siphonostele* (*amphi*, on both sides). Between the inner phloem and the central pith is a layer of inner endodermis.



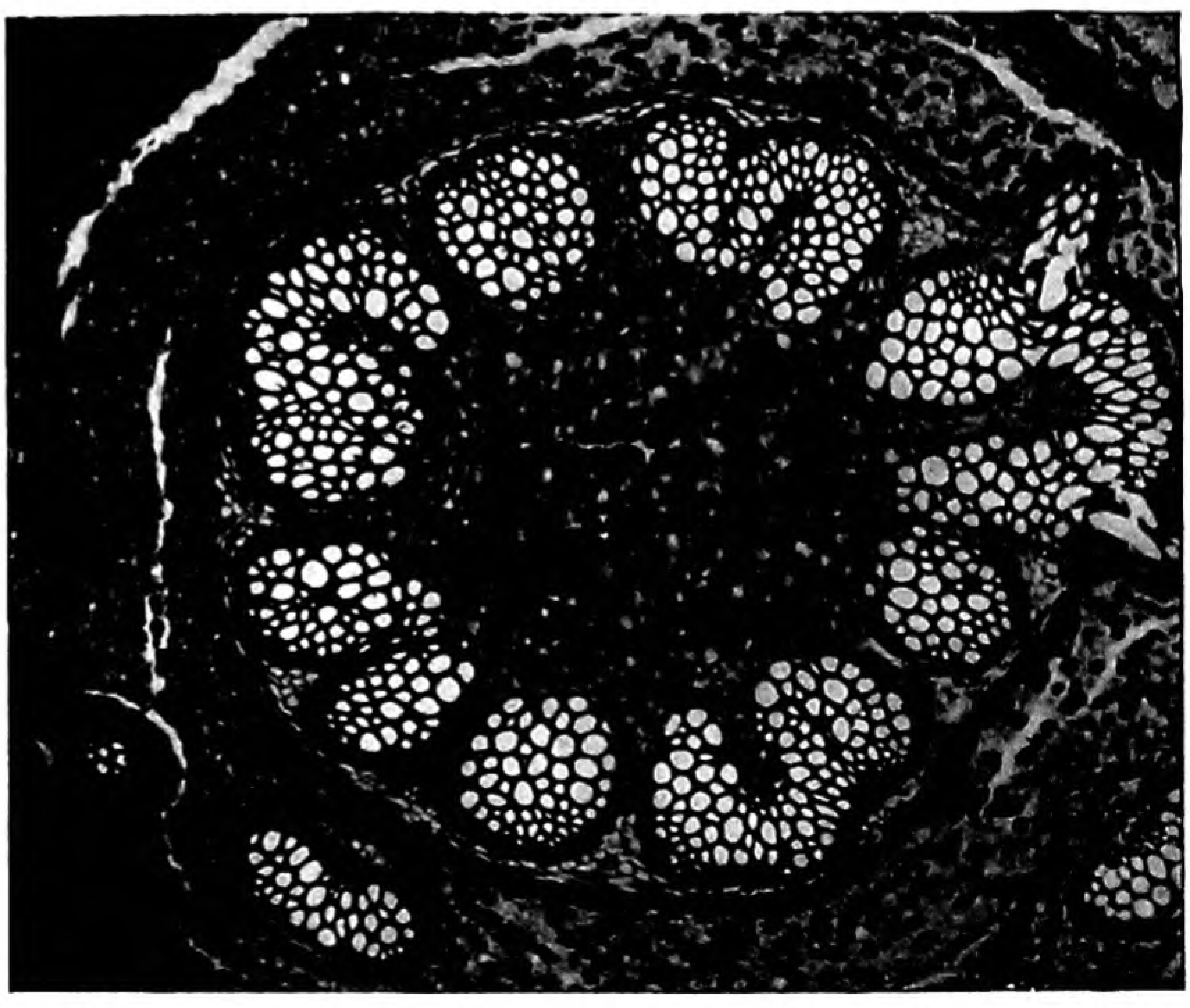
Leaf gaps and leaf traces. (*Top*) The xylem of a fern rhizome of the *Adiantum* type, showing the trace leaving the main body of the stele; also the leaf gap. (*Bottom*) Rhizome with adventitious roots, leaf gap, and bases of petioles.

A section of the rhizome of *Adiantum* cut at a node, as in the illustration, on p. 291, shows another important feature. Here the vascular tissue is in the form of a horseshoe. In front of the open end of the horseshoe, but not included in the photograph, is a *leaf trace*, that is, the vascular supply to a leaf. This arrangement results from the fact that just beyond the point where a leaf trace originates, a *leaf gap*, in which there is no conductive tissue, forms in the xylem and phloem. This gap is filled with pith cells.

When examining sections of a structure one should always try to visualize it as a body having three dimensions, and this method is of particular value in picturing the relations of leaf traces and gaps. The stele of *Adiantum* should be thought of as a cortex-covered cylinder which would be left hollow if the central pith were removed. The sections which show the vascular tissue in the form of a horseshoe happen to pass through leaf gaps. The illustration on the left shows this feature in diagrammatic form. Although the stem is a siphonostele the roots all have protosteles. This is the universal arrangement, whatever type may occur in the stems.

A somewhat more complicated siphonostele is found in *Osmunda*. The royal fern, the cinnamon fern, and the interrupted fern are three species that represent this genus. They are widely distributed and are well known because of their large size and striking beauty.

A cross section of the stem of one of these plants reveals not one but a considerable number of leaf gaps. Opposite each gap, as would be expected, is a leaf trace. So numerous and large are these pith-filled gaps that the vascular tissue takes the form of



Siphonostele of *Osmunda*. Note the numerous leaf gaps. Each gap has a leaf trace opposite it. Some of these, however, are beyond the edge of photograph.

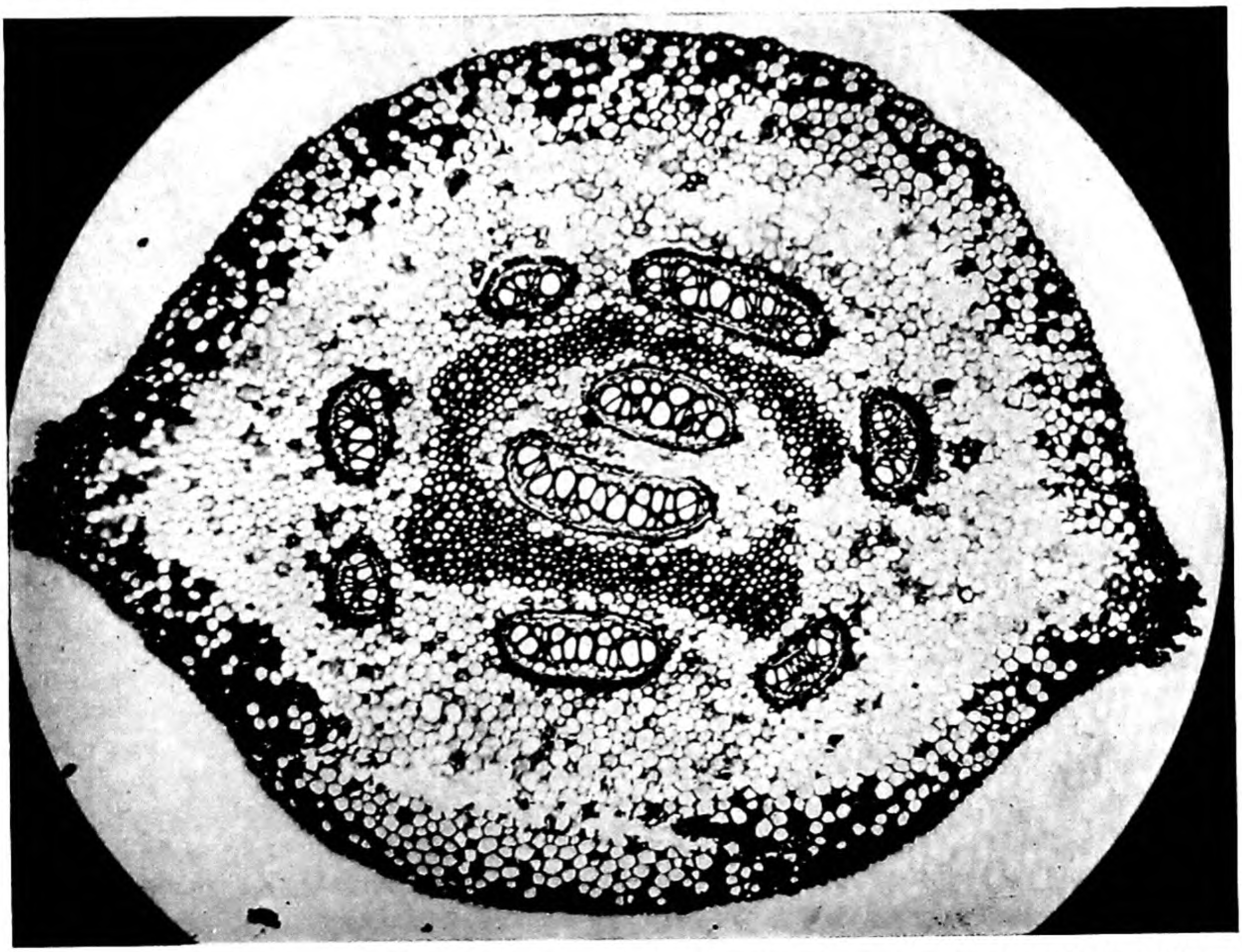
a *dissected siphonostele*. The leaf gaps are, in effect, wide rays, extending outward from the central pith.

In the stems of Osmunda, phloem occurs only outside the xylem. This is by far the more usual arrangement, not only in the ferns but in other plants as well. This type is commonly called the *ectophloic siphonostele* (*ektos*, outside). Exterior to the phloem there lies a pericycle and a rather definite endodermis.

THE SCATTERED STELE. The scattered stele is well represented in the common brake or bracken fern (*Pteridium*). This plant has a long, slender underground stem with the leaves spaced far apart. The sections of the rhizome are elliptical in outline and usually show two large vascular bundles near the middle and a number of smaller ones around the outer part.

Each bundle, having a core of xylem completely surrounded by phloem and pericycle and an individual endodermis, was once thought to be a complete protostele in itself and the structure was called a *polystele*. Recent studies have shown, however, that very young stems of this species have siphonosteles whose parts become disarranged in the older stems. It would seem now that this distribution of parts must be interpreted as a highly specialized development from the siphonostele.

THE SPORANGIUM AND SPORES. In most kinds of ferns the spores are produced in so-called "fruit dots" or *sori* (singular, *sorus*) on the leaves. Each sorus is a group of sporangia, often with a cover, the *indusium*. In many species, the leaves which bear spores are not otherwise different from the ordinary foliage but various degrees of specializa-



Scattered stele of *Pteridium*, made up of nine vascular bundles. A C-shaped zone of sclerenchyma encloses the two central bundles.

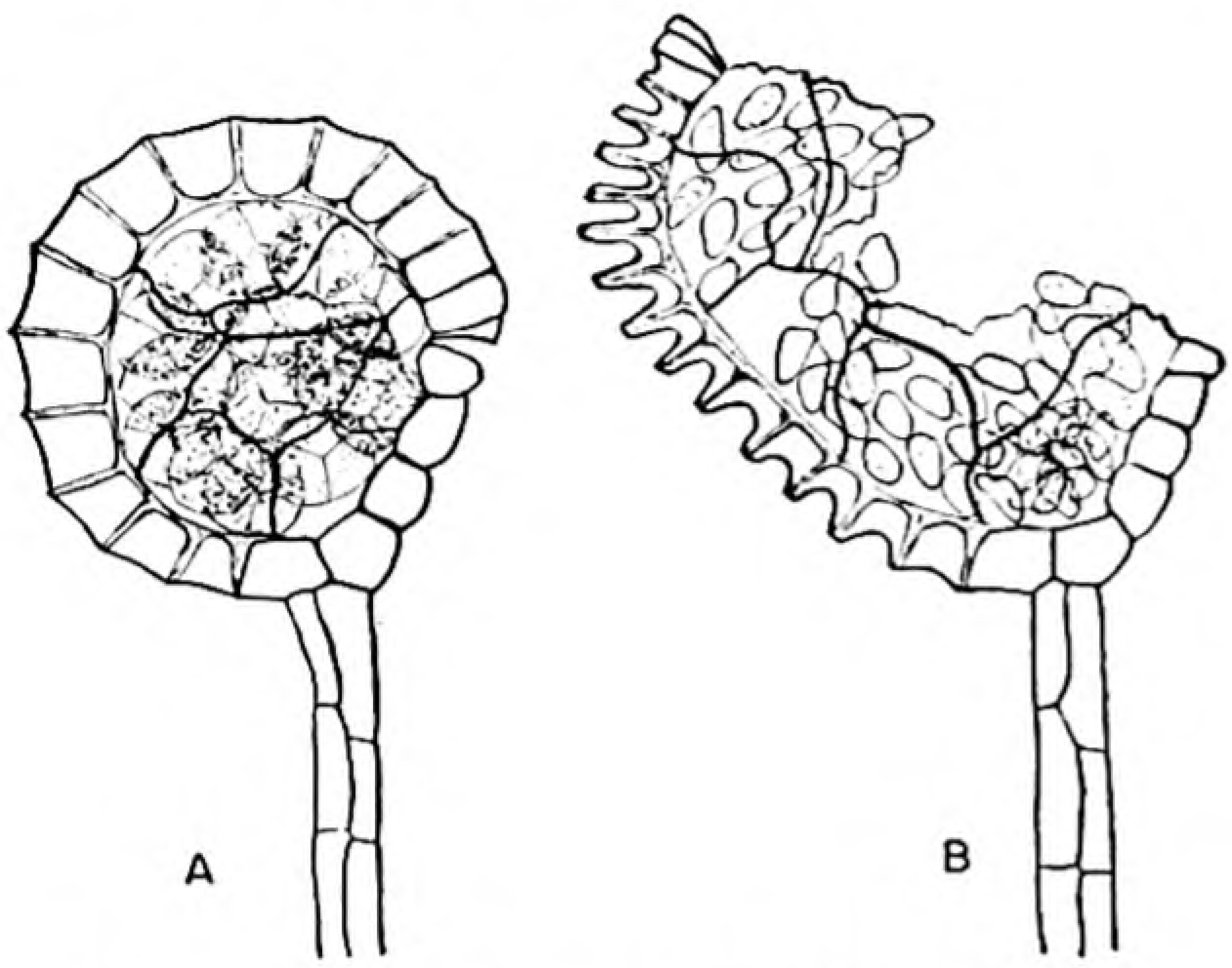
(*Left*) Tree fern from New Zealand rain forest illustrating extensive leaf development. (*Right*) *Onoclea struthiopteris* with foliage leaf and highly specialized sporophyll. (From Smith: "Textbook of General Botany." By permission of The Macmillan Company, publishers.)

tion occur, the spore-bearing leaves or leaflets of some retaining none of their foliage character.

Each sporangium contains a considerable number of spores. These are formed in tetrads from spore-mother cells, as a result of meiotic divisions. In the commoner species of ferns a single row of specialized cells making up the *annulus* extends part of the way around the sporangium, on the outside of its wall. These cells have greatly thickened inner and radial walls that play important roles in a peculiar behavior of the sporangium in discharging the spores.

When the mature sporangium is exposed to dry air it breaks open with a snap, the break occurring between two specialized *lip cells* opposite the annulus. After opening, it again snaps forward, throwing the spores. This action can be demonstrated very satisfactorily under the microscope by mounting mature, but still undried, sporangia in a mixture of water and glycerin and examining without a cover glass. The glycerin causes the water to diffuse out, in this way imitating the action of dry air. Because of the considerable amount of resistance in the mounting medium, a sort of slow

motion picture results, making possible accurate observations of the various movements involved. Careful examination of the illustration below will help to give an understanding of the machinery involved in throwing the spores.



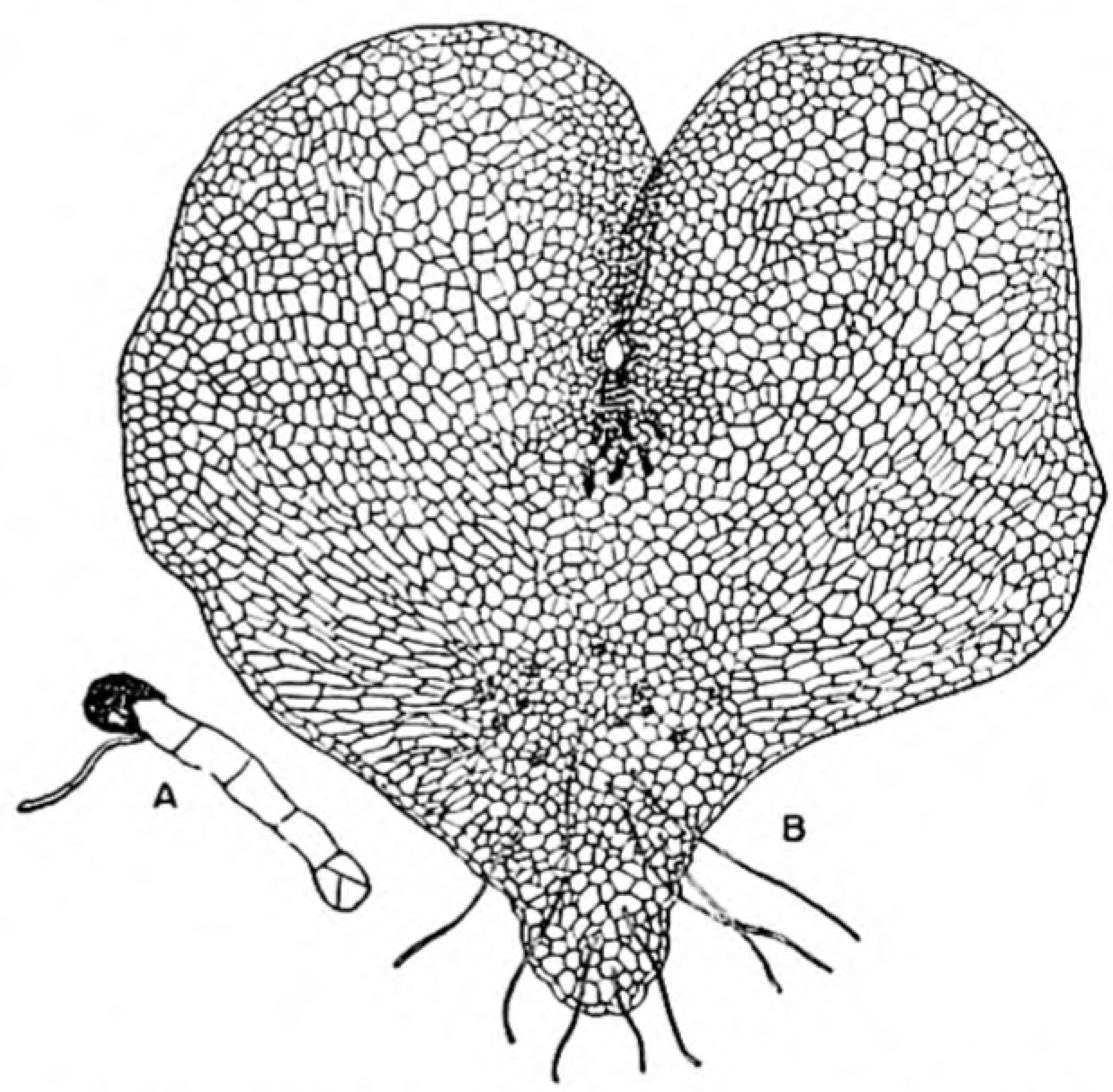
Fern sporangium. (A) Unopened, showing stalk, annulus (*at left side*), lip cells (*at right side*) and tetrads of spores. (B) The same structures in similar positions, but with sporangium open and spores ready to be thrown out.

The annulus is so constructed that its thin, flexible outer walls are drawn inward, largely by adhesion to the cell contents as they dry, thus shortening the outer part of the annulus and opening the sporangium. This shortening action results from the infolding of the outer walls which places the inner ones under stress, somewhat like the bending of a bow when the string is drawn. Thus, the sporangium opens against a considerable amount of tension. After a time the adhesive forces fail to hold and a vacuum suddenly forms in the cells of the annulus, allowing it to spring into its original position with a throwing action which scatters the spores.

The Gametophyte. The spore is the first cell of the gametophyte generation. When it falls into suitable moist soil it germinates, not into a leafy plant like the one that produced it, but into a small delicate structure that is seldom noticed except by a botanist. When it germinates it bursts its outer wall, exposing a single green cell. By a series of divisions a short filament is produced, made up of a row of chlorophyll-bearing cells and one or more rhizoids. Two or more oblique divisions in the terminal cell form a triangular *apical cell* and lay a foundation for the development of a flat prostrate *prothallium*. If it grows under favorable conditions, it usually assumes a lobed or heart-shaped contour and takes on the appearance of a small, delicate liverwort with numerous rhizoids on its lower side.

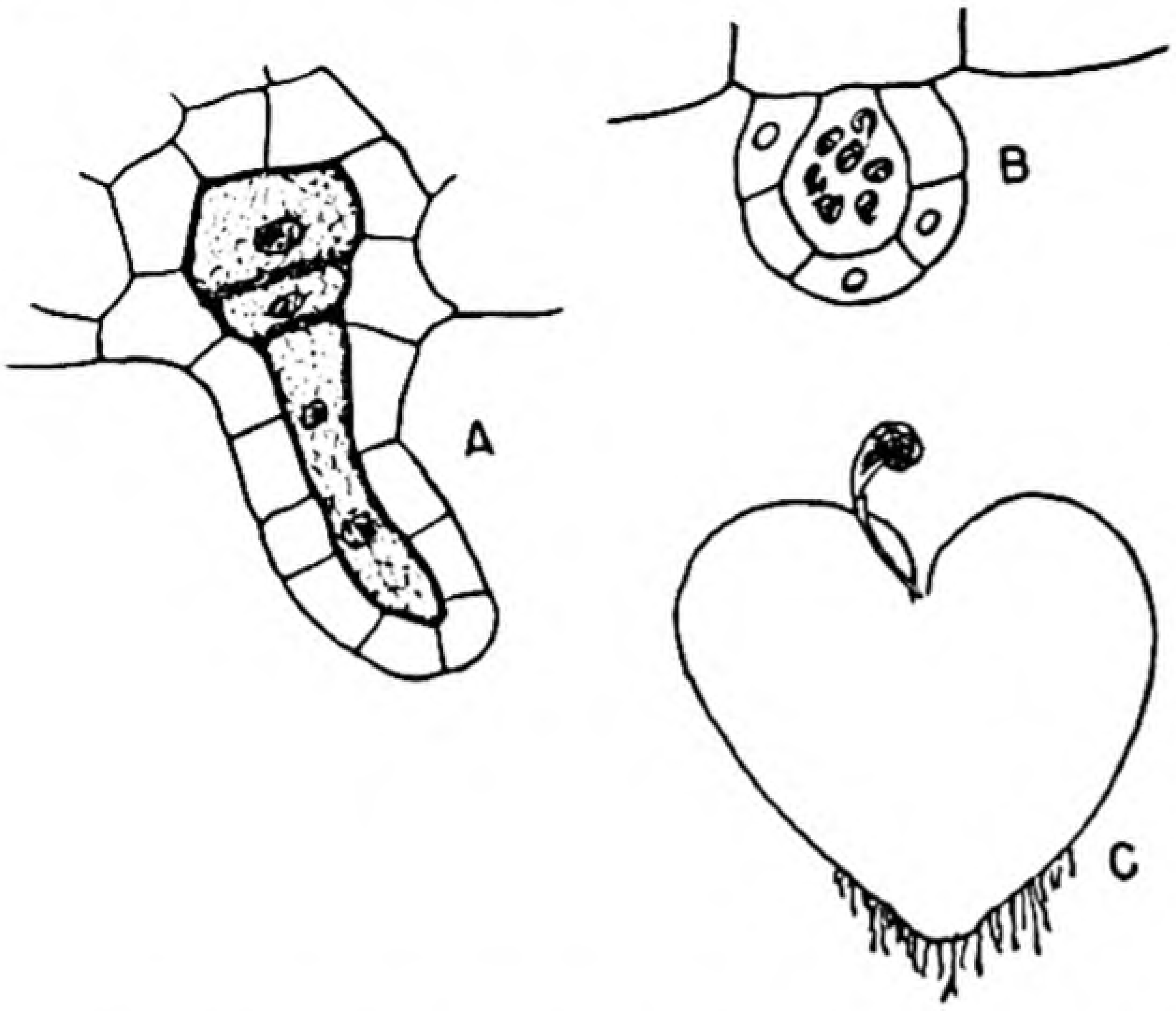
Living prothallia in various stages of development can be found sometimes in favorable places under fern plants growing naturally, and they occasionally become almost weeds in greenhouses. They can be grown by sowing spores on moist soil or on a brick or porous flower pot which is partly submerged in water and covered with a bell jar to prevent too rapid evaporation.

While the prothallia are still young, they begin to develop antheridia on their lower sides. Archegonia do not organize until the prothallium has become older and a thickened region, the archegonial cushion, has developed just behind the growing point. (See illustration B above.) In most ferns the prothallia are monoecious, but in some



Fern prothallia. (A) Young prothallium emerging from spore, showing a rhizoid and young apical cell. (B) Mature prothallium with archegonia near the notch and antheridia near the rhizoids.

species the male and female organs are on separate plants. Even in those which are potentially monoecious, if the prothallia are crowded, many of them remain small and irregular in shape and produce only antheridia.



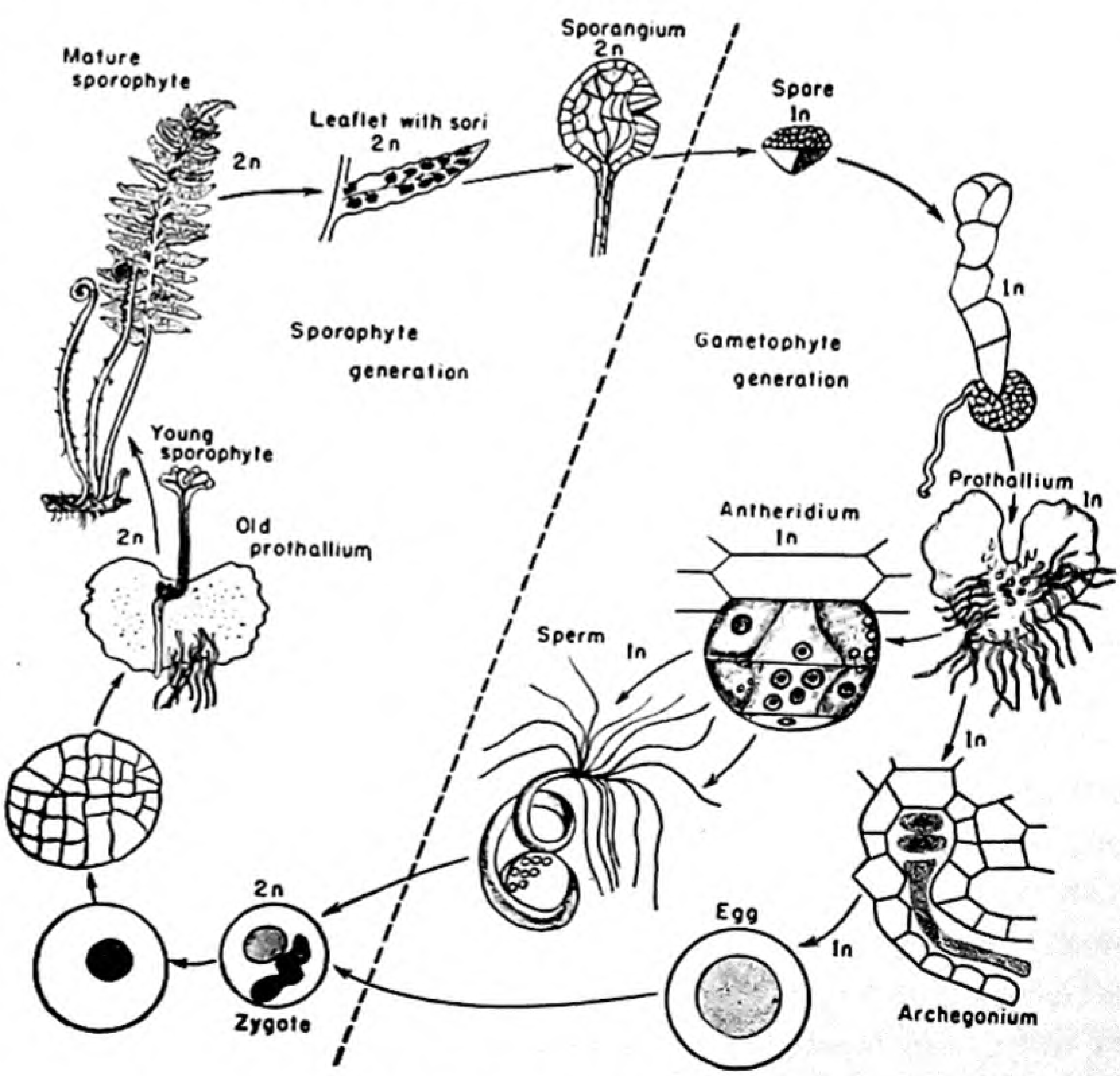
Archegonium, antheridium, and sporophyte of fern. (A) Archegonium, showing egg, ventral canal cell and neck canal cell with two nuclei. (B) Antheridium containing sperms. (C) Prothallium with young sporophyte attached.

The antheridium is a rounded or hemispherical structure attached directly to the thallus or borne on a short stalk. Its wall consists of three cells, although there seem to be more than three when seen from the outside or in section. This misleading appearance is due to the unique structure of the wall, for the two lower cells are in the form of rings, one on top of the other, and the hollow space within is covered by a dome-shaped cap cell. A single prothallium may produce a large number of antheridia, and although each one contains but few sperms, the total number is likely to be very large.

The archegonium is partly imbedded in the archegonial cushion, the prothallium being several cells thick in this region. The structure and relations of the different parts can best be seen in sections cut lengthwise through the plant. (See illustration A at left.) The curving neck, which is the only portion not imbedded, is much shorter than that of the archegonia of liverworts and mosses, and its canal usually contains a single binucleate cell.

Fertilization. As in the liverworts and mosses, fertilization cannot take place except by means of water. It is absorbed into the mature antheridia and archegonia, causing them to open, and a film of moisture is the medium in which the sperms travel. Under laboratory conditions, sufficient water for normal growth can be supplied to the soil without allowing it to wet the prothallia, with the result that fertilization can be prevented indefinitely. When the plants are allowed to become wet, however, many sperms may crowd into the open necks of the archegonia and in due time one unites with each of the eggs.

The Embryo. Very soon after fertilization the zygote divides three times, producing eight cells. These act in pairs, giving rise to the development



Life cycle of a fern.

of the four primary organs of the young sporophyte. From one of the quadrants produced in this way comes the first root of the plant and from another the first leaf. Another develops into the foot, a short-lived, rounded structure which imbeds itself in the archegonial cushion and absorbs food until the young sporophyte becomes independent. The remaining quarter of the embryo slowly elongates and becomes the forerunner of the rhizome, from which all the later leaves and roots arise. The first leaf of the embryo usually does not at all suggest the type which is characteristic of the species, but those arising from the rhizome show a series of transitional stages to the adult form. With the production of spores, the life cycle is completed. (See illustration on p. 296.)

The Origin and Evolution of the Pteropsida. In Chapter 18 it was pointed out that the Psilopsida apparently originated as the first true land plants in Silurian times and that by about the middle of the Devonian Period a considerable number of genera and species had arisen. It was also stated that there are still a few species of living plants that seem to be the slightly changed descendants of some of those ancient forms.

In discussing the apparent relationships among those Devonian Psilopsida, certain strains were mentioned that seemed to merge almost imperceptibly into the Sphenopsida with their jointed stems, while others developed the characteristics that finally became established in the Lycopsida.

At about the time the Sphenopsida and Lycopsida were emerging, a much more important branch of this ancient stock seems to have been taking form. This branch was to evolve into the division known as the Pteropsida and was to become differentiated into the three great branches of modern vascular plants, the Filicineae, discussed in this chapter, and the Gymnospermae and Angiospermae considered in Chapters 20 and 21.

It is possible that *Psilophyton* of early Devonian times may be in the line of descent of the ferns from the Psilopsida. Fossils belonging to this genus have been collected from such widely scattered localities as Quebec, New York, Wyoming, Scotland, France, Belgium, and Norway. One cannot but reflect upon the widespread distribution of this genus in such ancient times. A glance at the North Polar map on p. 171 gives some idea of the great distances traversed by this plant.

Psilophyton had all the essential features of *Rhynia*, such as a rootless, dichotomously branched rhizome with upright leafless shoots and also with forked branches and a simple protostele. Three features, however, set it off from *Rhynia*. The sporangia occurred in pairs that recurved somewhat, the stem was covered with prickles, and the young shoots uncoiled in the form of loose spirals, suggesting a sort of circinate vernation. These plants were 2 or 3 feet tall.

The simplest Filicineae appeared in mid-Devonian times. These plants had stem structures much like those of the Psilopsida but certain small, dichotomously branched parts had thin extensions across the gaps between the branchlets, forming leaves or leaflets. Such a structural development is found in the fossil genus, *Cladoxylon*. Simple sporangia, much like those of *Rhynia*, formed on tips of many of these branchlets, that is, at the margins of the primitive leaves.

Such fossils lead many botanists to think the large, broad leaves of modern ferns are actually the culmination of a series of steps that have brought about the evolution of leaves from stems. If this interpretation is correct, the dichotomously branched veins of present-day ferns correspond more or less closely to the smallest twigs of such ancient plants as *Rhynia*. Leaves of this type with a complicated system of veins are called *macrophylls* (*makros*, long or large; *phyllon*, leaf). These contrast sharply with the much simpler *microphylls*, (*mikros*, small) of the lycopods (see p. 285). One other even more important distinction is that macrophyllous plants always have leaf gaps and microphyllous plants have not.

By the end of the Paleozoic Era a considerable number of new forms of ferns had appeared, and during Mesozoic times this division reached its culmination. Since then, seed plants have become gradually more prominent and the ferns appear to be slowly losing importance.

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Campbell, "Mosses and Ferns."
Eames, "Morphology of Vascular Plants."
Eames and MacDaniels, "An Introduction to Plant Anatomy."

Chapter 20

PTEROPSIDA: GYMNOSPERMAE

The class, Gymnospermae, is made up of a group of orders that seem to be very closely related. Beginning near the end of Devonian times and continuing for some hundreds of millions of years into the Mesozoic Age, two rather distinct lines of descent appear to have been developing as specialized branches out of the seed-fern stock, or Cycadofilicales. One of these branches began with the Bennettitales which seem to have given place finally to the modern cycads. The other began with the Cordaitales, an order which gave rise to the modern conifers and that "living fossil," *Ginkgo*.

During a long period of time, especially in the latter part of the Paleozoic Era, the gymnosperms were the dominant vegetation of the earth, but by the end of the Mesozoic, the angiosperms were occupying much of the ground formerly held by the gymnosperms. At the present time, although the conifers control considerable areas, the angiosperms are gradually succeeding them as the dominant world vegetation.

The following are the main topics discussed in this chapter:

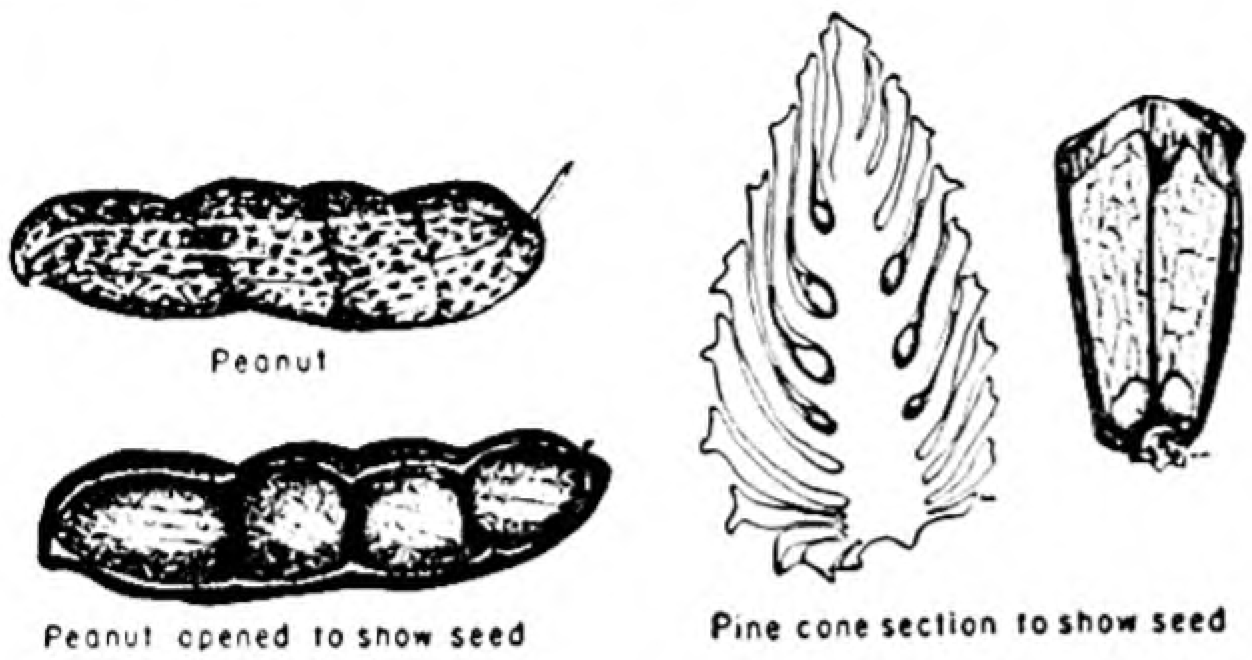
- Modern Gymnosperms
  - Coniferales
  - Cycadales
  - Ginkgoales
  - Gnetales
- Ancient Gymnosperms
  - Cycadofilicales
  - Cordaitales
  - Bennettitales
- Relationships Among Gymnosperms

It has been customary to set off into a group the more or less complex plants which reproduce by means of seeds. If we were to consider only the species which have living representatives on earth today, the line between those which bear seeds and those which do not could ordinarily be sharply drawn. But when the fossils are taken into consideration, other characteristics prove to be so important that seed production, while relatively significant, is only one of several criteria by which to recognize relationships. In fact, the fossil record shows that certain members of some of the ancient groups at one time produced seeds while the modern representatives of these same divisions are now entirely devoid of such structures. This statement applies both to the club mosses and the ferns.

Ignoring for the moment the fossil records and comparing modern seed plants, it is found that they fall into two rather distinct natural groups. These groups are angiosperms and gymnosperms. The following explanation should make clear the more obvious of the distinctions between them, and the present chapter and the next, when taken together, will point out some of the fundamental differences.

The seeds of common plants develop inside a pod or other container. This arrangement can be

recognized easily in such well-known foods as tomatoes, beans, peanuts, peaches, and lemons. Even in many plants like the sunflower and the various grains detailed study shows that the outer



Contrast between seed production of angiosperms and gymnosperms. The peanut is an angiosperm. Its shell is the ovary wall. The pine cone is cut lengthwise to show position of seeds on scales. (*Right*) A scale with its two seeds. Note that seeds of a gymnosperm do not form in a closed container.

coat (pericarp) is a protective covering external to the seed. All those plants with enclosed seeds are angiosperms (*angeion*, a vessel; *sperma*, a seed).

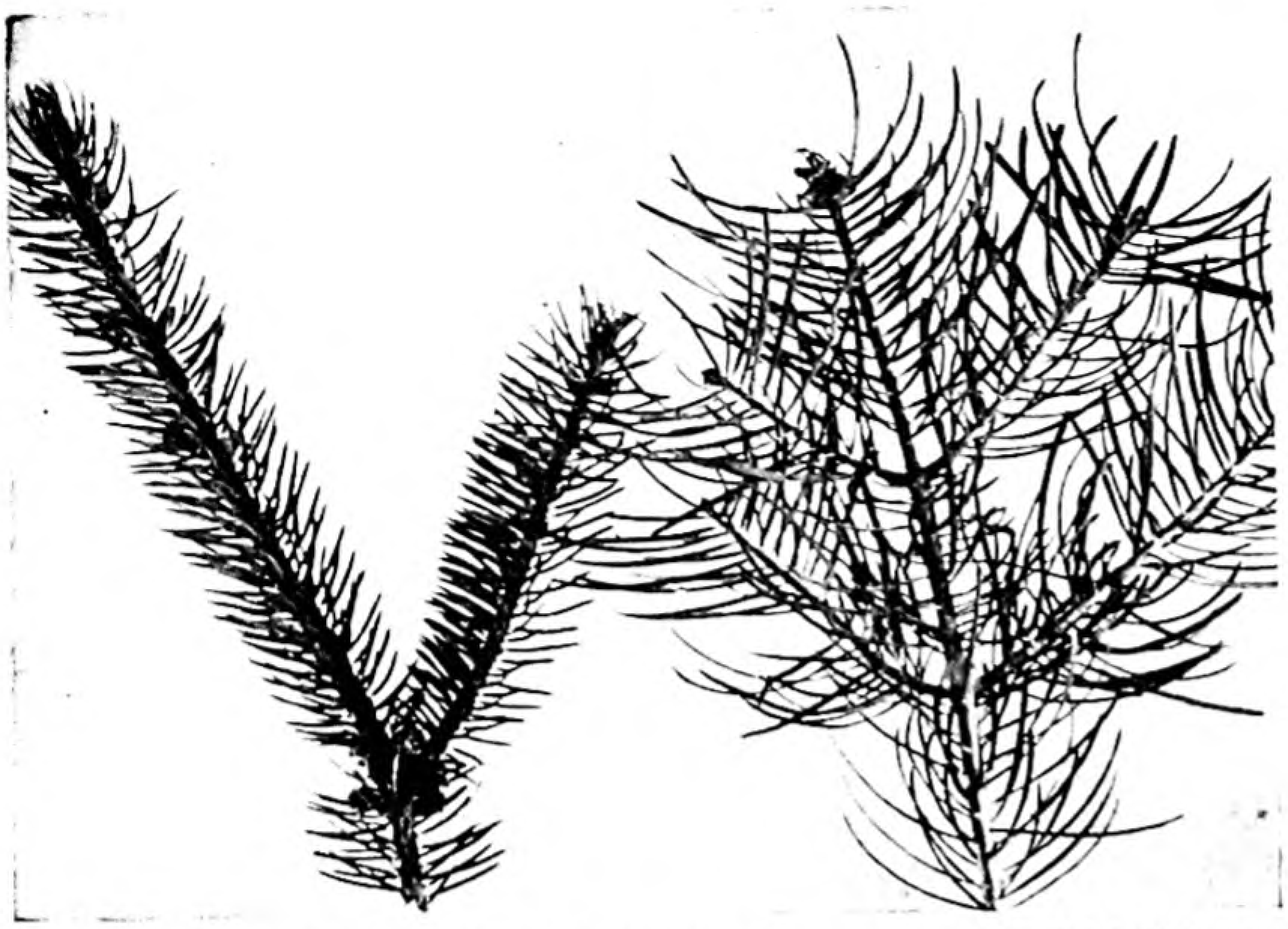
The gymnosperms, on the other hand, have more or less completely exposed seeds. This arrangement can be demonstrated by cutting or breaking in two a nearly mature cone from a pine, fir, or spruce tree. It consists of numerous scales which are arranged in close-fitting spirals around an axis. Fully exposed on the upper side of each scale, often called the *ovuliferous scale*, will be seen one or two seeds. Although they are far down toward the axis and are protected by the outer parts of the cone, they are not encased in a closed vessel. The word, gymnosperm (*gymnos*, naked), refers to the fact that plants of this type have seeds that are not protected by a pod. In some species the seeds are very much more exposed than they are in the pines.

MODERN GYMNOSPERMS

The class, Gymnospermae, includes four orders of living plants. They are the Coniferales, the Cycadales, the Ginkgoales, and the Gnetales. In addition, three other orders, the Cycadofilicales, the Bennettitales, and the Cordaitales, are now known only from their fossil remains. These will be discussed later in this chapter.

Coniferales. Such widely distributed trees and shrubs as the redwoods, larches, pines, spruces, firs, junipers and bald cypress of the Northern Hemisphere and the podocarps and araucarias of

Four terminal bud scars on pine (*Pinus edulis*) with a fifth just at the bottom of the photograph, indicating that the oldest leaves shown are five years old.



Other conifers. (*Left*) Twig of Colorado blue spruce. (*Right*) White fir.

The trees are the most important constituents of extensive forests, especially in the colder parts of the North Temperate Zone. In North America a great band, largely of spruces and firs, interspersed with tamaracks in the peat bogs, stretches from Maine and Labrador to British Columbia and Alaska. The northern parts of these forests extend into the Arctic regions where the trees are smaller, and at their extreme northern limit, even dwarf. Throughout this belt of gymnosperm trees there are considerable numbers of birches and aspens, both angiosperms. These great forests, the famous "northern woods," are important sources of lumber, especially pulpwood.

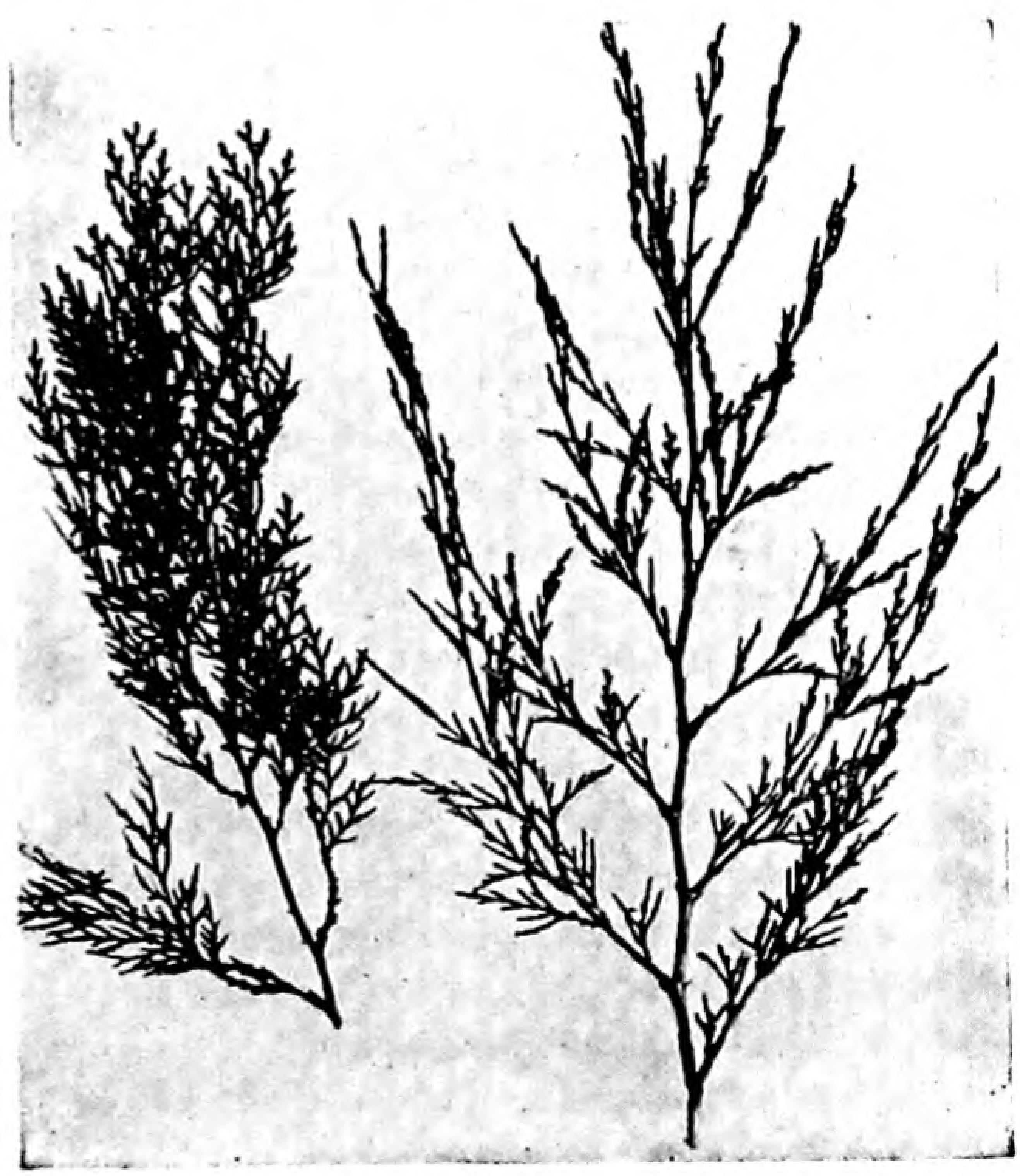
the Southern Hemisphere belong to the Coniferales. This order takes its name from the fact that the seeds are produced in cones or in structures which may be interpreted as such. The vast majority of the conifers are evergreen, although tamarack and bald cypress are deciduous.

It should be understood that both gymnosperms and angiosperms include both evergreen and deciduous species. While most angiosperms drop their leaves in the winter, a few, such as the live oaks and magnolias of the southeastern United States, the evergreen chaparral of the West Coast, and trees of the Tropical Rain Forests, retain the green leaves of one season until new ones are formed the next. Hence these plants are always green, that is, evergreen.

An inspection of the twigs of an evergreen conifer shows that in most species the leaves remain alive and firmly attached until they are several years old, but that the oldest die and fall off every year. The youngest leaves are at the ends of the twigs and those that are dying are farther back from the growing tips. By counting the terminal bud scars on the twigs it is possible to determine the age of the oldest leaves.

All the conifers are woody plants. The vast majority are trees, but a few, such as the alpine juniper and some species of yew are low shrubs.

Coniferous forests extend southward into mountainous regions of the United States where high altitudes are responsible for low temperatures and



Scale-leaved conifers. (*Left*) Arbor vitae. (*Right*) Juniper.

Bald cypress twig with leaves.

other rigorous elements duplicating to some extent those of Arctic regions. In these mountains the spruces reach timberline, often responding to the hard living conditions by growing prone on the ground.

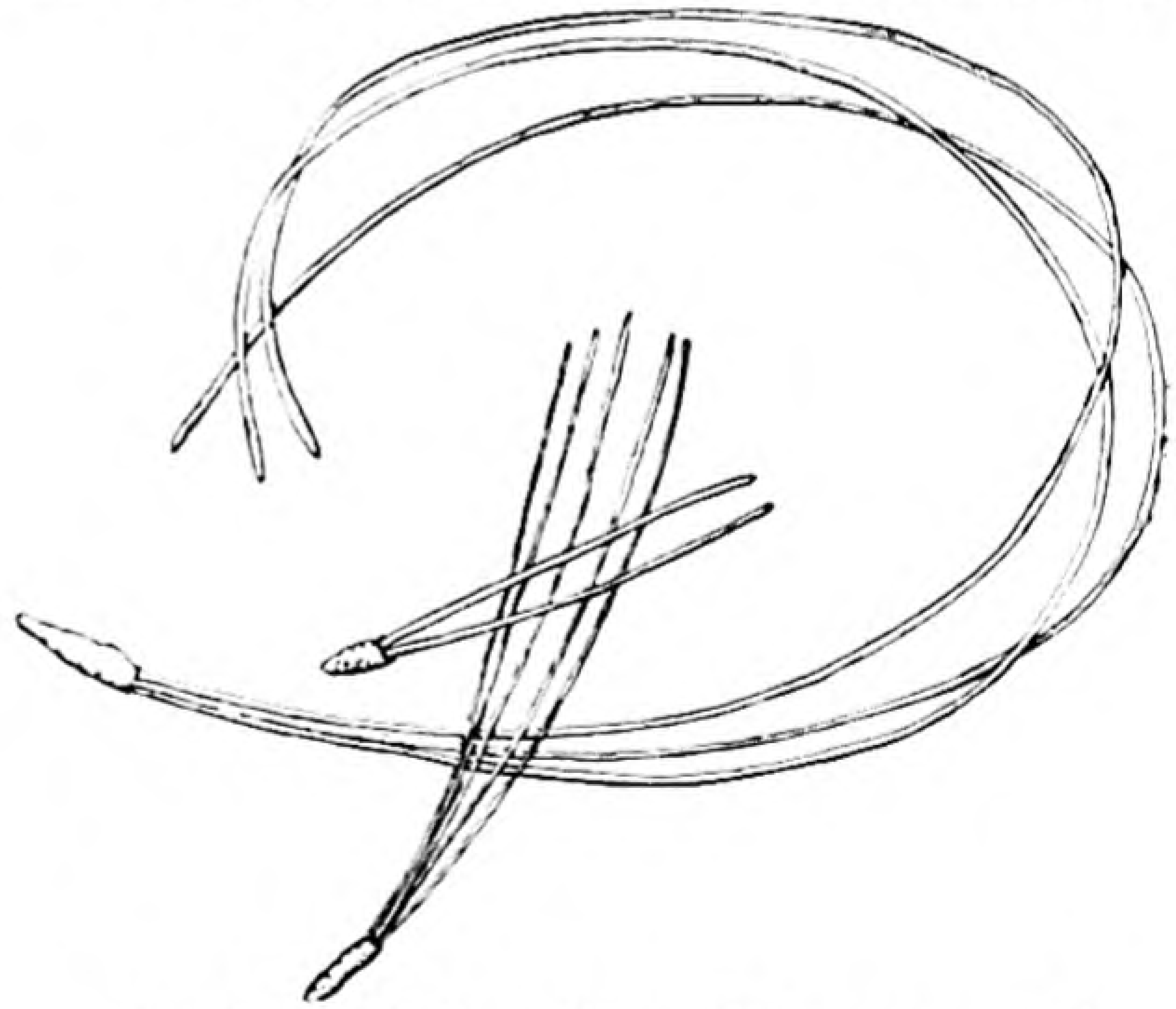
In the western and northwestern United States, Douglas fir and several species of pine mingle with the spruces and firs and extend the range of the conifers still farther south; near the coast are arbor vitae and hemlocks.

The most striking members of the gymnosperms are the two species of *Sequoia*, commonly known as the giant trees (*Sequoia gigantia*) and redwood trees (*S. sempervirens*) of restricted distribution in California. These are the remnants of a genus which was widely distributed in earlier geologic times. Measures have now been taken to make sure that they will not become extinct. Some of these trees are probably the largest and oldest living individual organisms on earth today.

In the swamplands of the southeastern United States there are several other important conifers. Perhaps most characteristic of these is the bald cypress (*Taxodium distichum*) which grows in water up to several feet deep. The base of the trunk is always swollen and the roots often have upright extensions, called "knees." In the same region there are several fine species of pine trees that are sources of both lumber and turpentine. Most important of these is the longleaf pine, *Pinus palustris*, while of less value are the shortleaf (*P. echinata*) and loblolly (*P. taeda*) pines.

The commoner conifers are easily recognized by their leaves which are often called needles. Those of the spruce, fir, and hemlock are arranged spirally, one in a place, on the twigs. The leaves of spruce are stiff and sharp, and square in cross section; those of hemlock and fir are softer, flattened, and less pointed.

A number of genera have short, scalelike leaves which are sometimes closely appressed to the twigs. Among these are the true cedars of western Asia and the Mediterranean region; the "red cedar" of eastern North America, which is really a juniper; the junipers of the Rocky Mountain region; and the various species of arbor vitae of both the Eastern and Western Hemispheres. The round, bluish berries of the junipers, and the thick, fleshy fruits of some species of arbor vitae do not seem to belong to conifers, but an examination of these



Pine leaves. Piñon, *Pinus edulis*, a two-needle pine. White pine, *Pinus strobus*, a five-needle pine. Long-leaf pine, *Pinus palustris*, a three-needle pine.


Ovulate cones of western yellow pine, *Pinus ponderosa*. (*Left*) Cluster as seen in June of first year. (*Right*) One-year-old cones.

structures during development shows that they are modified cones.

Two genera, including the tamaracks of North America and Europe and the bald cypress of the Southern United States are peculiar in that most of their species are deciduous. These trees resemble other conifers in habit and, in the summer, would be mistaken for evergreens. Tamarack has some of its leaves crowded together on short spur branches and others scattered singly on rapidly growing twigs. In bald cypress the feathery, leafy twigs, rather than the individual leaves, fall from the branches at the end of the growing season.

It is usually easy to distinguish the pines from other evergreen conifers by the arrangement of their leaves (needles) in groups of two, three, or five. A scaly or chaffy wrapping is around the extreme base of each bundle. Detailed study of the structure of these leaf bundles shows the base to be a dwarf branch which is incapable of growing in length, but with the leaves arising from its summit. The white pines usually have groups of five leaves although occasionally there may be more, while other species commonly have groups of two or three. One southwestern tree is sometimes described as having one leaf in the bundle and is accordingly given the technical name, *Pinus monophylla*. That this is really a variant of the common piñon, a two-leaved pine of the region, is shown by the fact that both types of leaves sometimes occur on the same tree. Pine needles vary in length from less than an inch in some of the scrub pines to as much as 16 in. in the southern longleat pine.

A cross section of a leaf is semicircular or triangular, depending upon the number in the bundle, the whole cluster tending to be cylindrical (see illustration on p. 31).

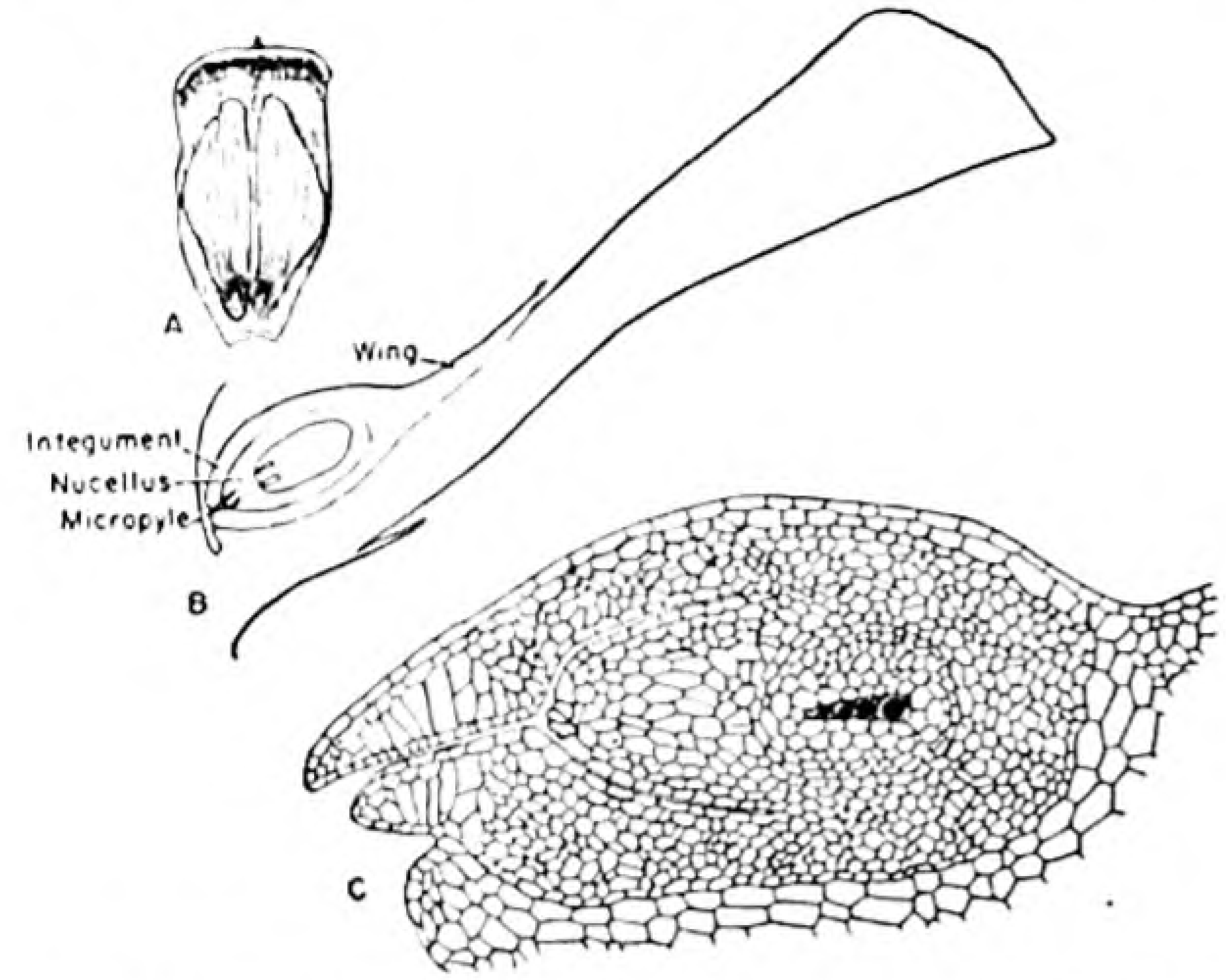
Life Cycle of Pinus. There are few sections of the North American continent where either native or planted pines cannot be found. For this reason these trees furnish a good basis for an understanding of the conifers. The white pine, once so common in the Eastern States and in the region of the Great Lakes, the western yellow pine and sugar pine of the West, the piñons or nut pines of the Southwest, the longleaf and loblolly pines of the South, and the introduced Austrian pine, widely used as an ornamental, are among the better known species.

The tree, which is the sporophyte generation, produces cones of two kinds; *staminate* and *ovulate*. The former bear the *microspores* or *pollen grains* and the latter form *megaspores* in the interior of the ovules.

THE OVULATE CONE. Early in the growing season very small ovulate cones commonly form near the tips of some of the young shoots of pine trees. An examination of one of these little cones shows it to have several ovuliferous scales each of which normally has two small ovules attached to its upper surface near its place of attachment to the axis. The ovules are the forerunners of the seeds.

When examined with a magnifying glass a young ovule has the appearance of a small pearly white object attached to the ovuliferous scale. The main body of the ovule is the *nucellus* or megasporangium, and a covering layer, the *integument*, which grows collarlike around it. The integument is met here for the first time because it does not occur in

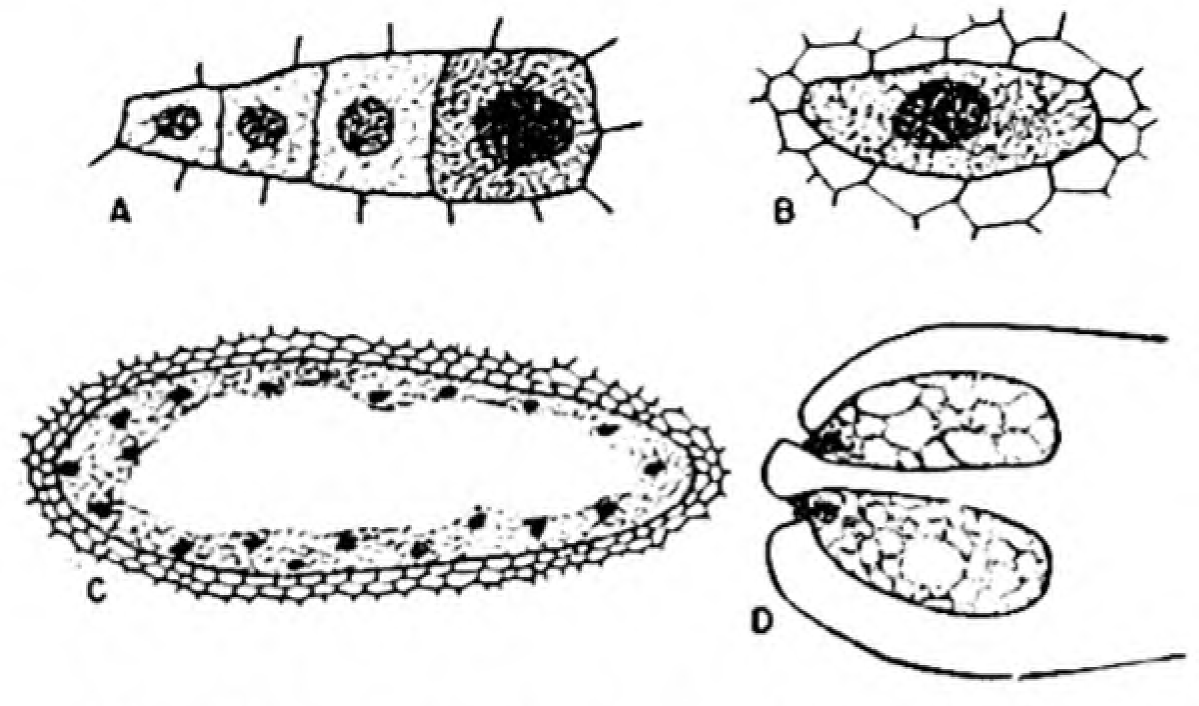
any of the lower groups of vascular plants. The parts within it, however, are very similar to the megasporangia and megaspores in the various



Ovules of pine. (A) Ovuliferous scale with two winged seeds. (B) Section through ovuliferous scale with ovule forming. Within the nucellus is the female gametophyte with two archegonia. (C) Young ovule showing integument with micropyle, and the nucellus containing linear tetrad of megaspores.

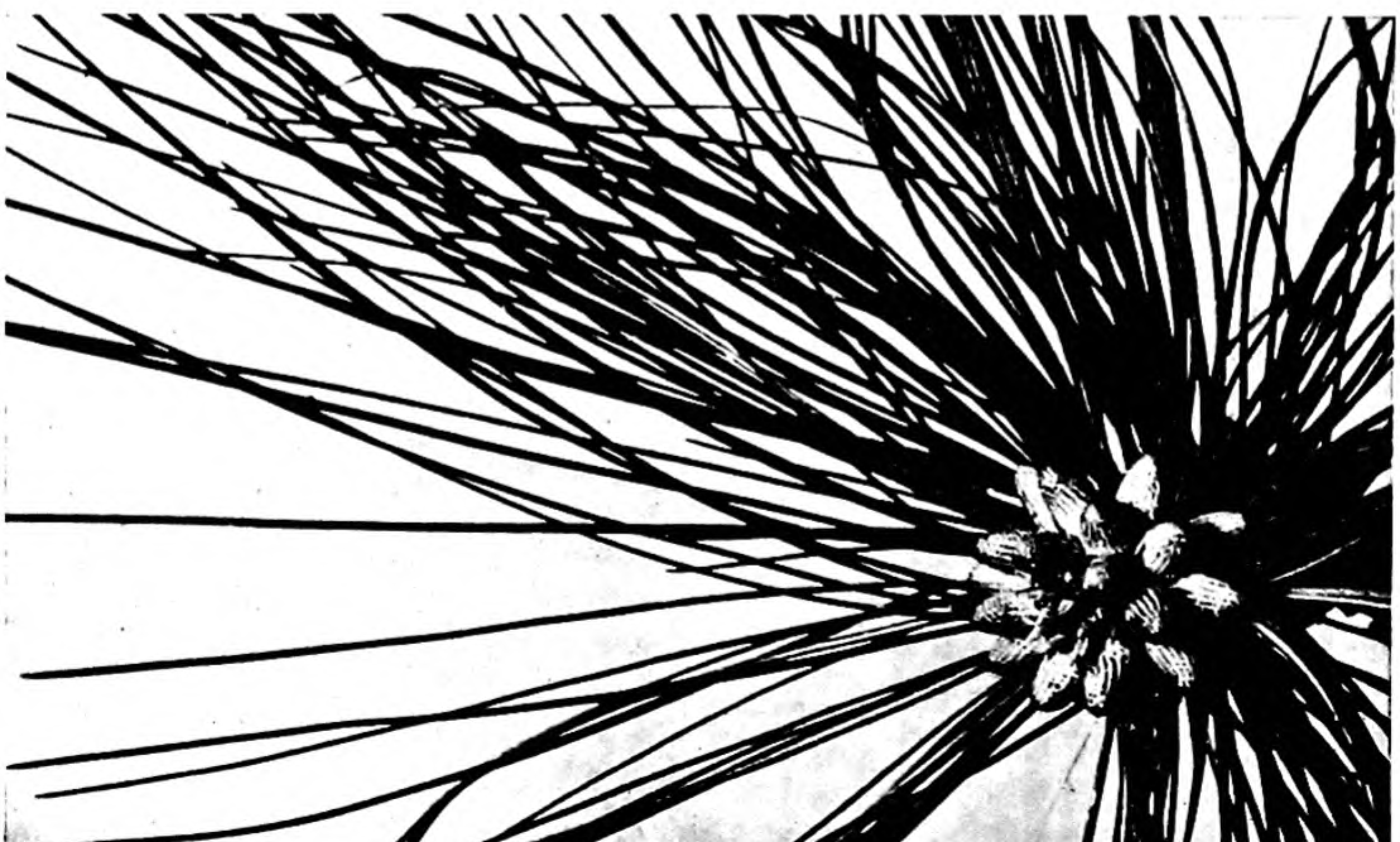
heterosporous forms such as *Selaginella* already studied (p. 283).

The integument never quite covers the nucellus, but leaves a small opening which is known as the *micropyle*. This opening is of great importance be-



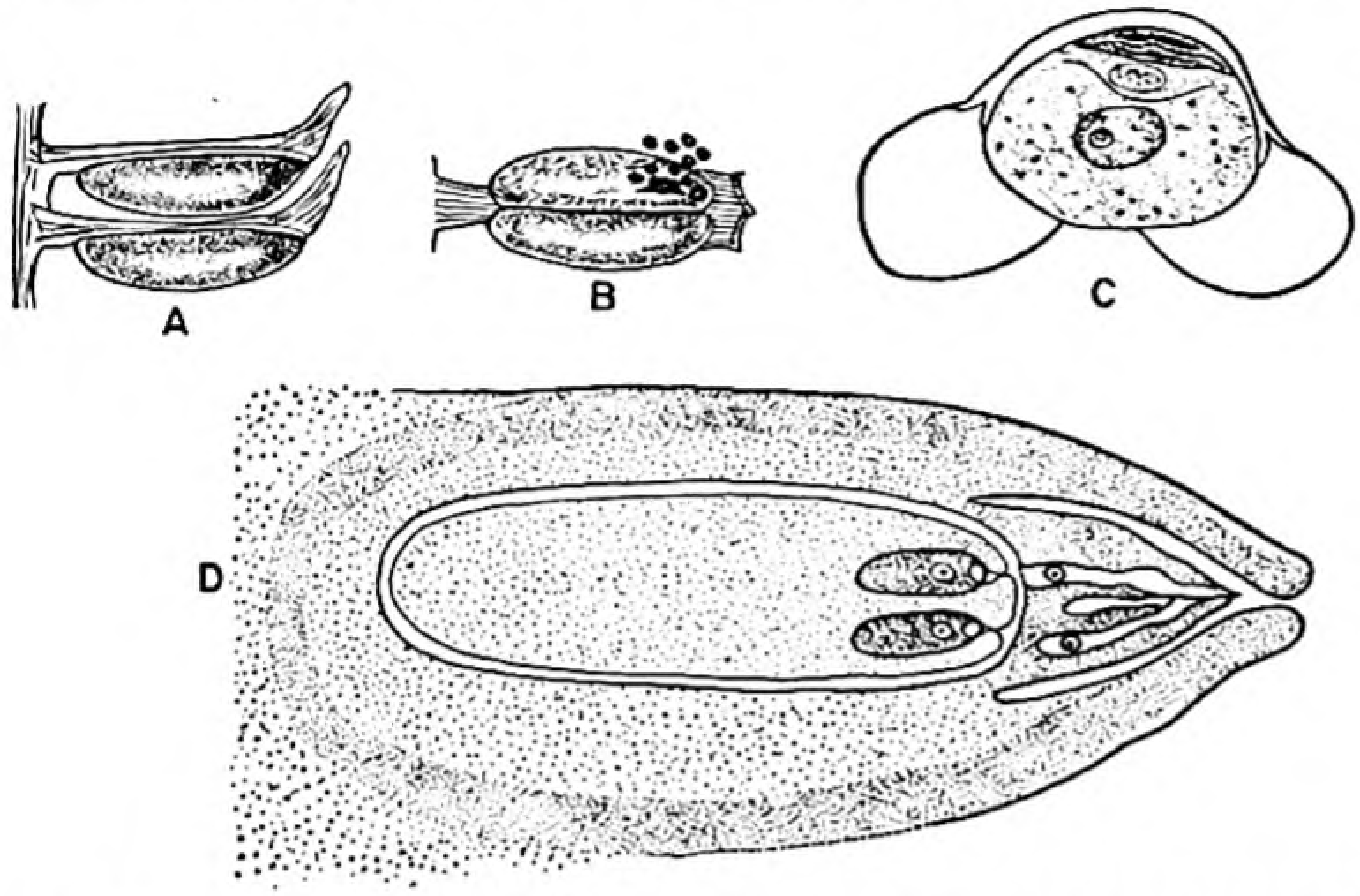
Female gametophyte of pine. (A) Linear tetrad of megaspores. (B) One megaspore replacing others. (C) Free nuclei of female gametophyte. (D) End of female gametophyte with two archegonia.

cause the wind-borne pollen grains which fall between the scales, enter into the ovule through it after this manner: At the time when pollen is being shed, the scales of the young ovulate cones separate to some extent, permitting the grains to enter. At the same time, a droplet of liquid, secreted by the nucellus, fills the micropyle. Pollen grains coming in contact with this liquid adhere to it



Cluster of staminate cones of western yellow pine.

and are drawn through the micropyle as the droplet dries, finally becoming attached to the surface of the nucellus where they gradually organize mature male gametophytes. Details of this phase of the life history are given in following pages.



Male gametophytes of pine. (A) Two staminate scales, each with a large microsporangium, as seen in profile. (B) A scale as seen from below, with pollen grains escaping from one microsporangium. (C) Male gametophyte at about the time it is shed from pollen sac. (*Above*) Remains of two cells that are disintegrating, followed by the generative cell. The tube nucleus is lowest of the four. Note the large hollow floats at sides of pollen grain. (D) Pollen tubes as seen in section of ovule. Pollen tubes approaching archegonia, about a year after pollination took place.

Early in the development of the ovule one cell begins to enlarge deep within the nucellus. It finally becomes conspicuous and begins to absorb some of its neighbors. Its behavior soon shows that it is a spore mother-cell, for meiosis takes place. But instead of the type of tetrad that forms in the lower plants, a row of four megaspores takes form. The three of these nearest the micropyle now gradually disappear and give place to the one nearest the *chalaza* which is the attachment of the ovule to the scale. This single megaspore develops into a mature female gametophyte much after the manner of that in *Selaginella*.

THE FEMALE GAMETOPHYTE. As the megaspore germinates, forming the female gametophyte, there is at first a period of *free nuclear division*, that is, a time when nuclei divide mitotically but walls do not organize between them. During this time, surrounding cells are absorbed, resulting in a large protoplast containing many nuclei. Cell walls are now formed, and the young gametophyte becomes organized into a solid mass of tissue, which continues to grow and absorb the nucellus until it occupies the greater part of the volume of the ovule.

By a series of steps, a number of archegonia are now formed at the end of the gametophyte nearer to the micropyle. They are completely imbedded in the gametophyte. Each contains a large egg, and, at its top, a short-lived ventral canal nucleus and a very rudimentary neck. The egg is now ready for fertilization, but before interpreting that important process it is necessary to return to the pollen grain and male gametophyte.

THE STAMINATE CONE. At about the time when the young ovulate cones become organized, numerous staminate cones reach maturity. These are easily recognized by peculiarities in shape, color, and arrangement, and especially by the fact that their scales are much more numerous than are those of ovulate cones. Both staminate and ovulate cones usually grow on the same individual tree, although not on the same twigs.

The pollen is shed as soon as it is mature. The grains are small and dry, and are carried by the wind. In the great forests of pine and other evergreen trees the pollen is so abundant at shedding time that it causes the appearance of a yellow haze in the air and occasionally it settles as a perceptible layer of dust on city streets miles away from the forest in which it is produced. Almost all of it is wasted in so far as its value to its species is concerned, and the infinitesimally small amount which sifts in between the scales of the ovulate cones is all that plays any part in reproduction.

THE MALE GAMETOPHYTE. Two sporangia develop as enlargements on the under surface of each scale of the young staminate cone. As time goes on, considerable masses of pollen mother-cells are organized and then by meiotic divisions each forms

a tetrad of pollen grains. Obviously, these are microspores and therefore belong to the gametophyte generation.

Each pollen grain has a pair of balloon-like floats which are simply hollow extensions from the spore wall. Soon after the tetrads have formed, the pollen grains separate from each other; the sporangium wall, often called the *pollen sac*, breaks open; and the pollen floats out into the air where it may be carried in any direction by air currents.

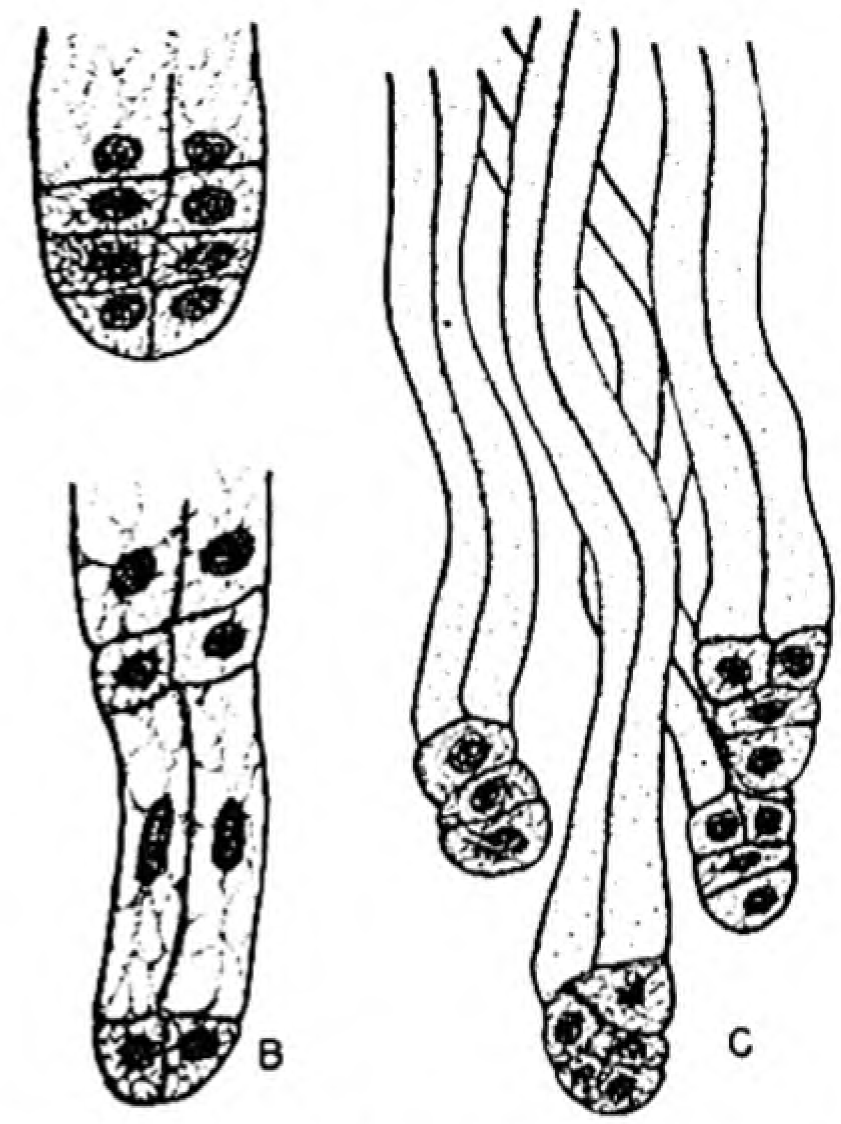
At shedding time the microspore has begun its development as a male gametophyte. Already several cell divisions have taken place and there are likely to be the remains of one or two small lens-shaped cells that were cut off by mitotic division but are in the process of vanishing without having carried on any apparent functions. Two important nuclei remain, however, and are called, respectively, the *tube nucleus* and the *generative nucleus* (see C in the illustration on p. 305).

All the pollen that does not chance to enter the micropyle of some ovule soon dies. On the other hand, those rare individual microspores that reach their destination have the prospect of a long career. Strangely enough, the pollen grain, now almost a mature gametophyte, does not become entirely mature and shed its sperms until a full year later. Instead, the development that has been taking place almost ceases. The only change of consequence is the production of a short *pollen tube* as an outgrowth from the grain. It slowly digests its way through the nucellus during the summer months, only to be stopped by winter before it has reached all the way through this almost microscopic mass of cells.

The next spring, a year following the time of pollination, sees renewed activity on the part of both gametophytes. It is at this time that archegonia, each with its egg, are organized in the tissues of the female gametophyte (see D in the illustration on p. 304). At about the same time a direct descendant of the generative nucleus divides mitotically, making two *sperm nuclei*.

FERTILIZATION. When the eggs in the archegonia and the sperms in the pollen tubes are fully mature, the pollen tubes grow until they come near the archegonia. At this time each pollen tube breaks open and liberates the sperm nuclei into the cytoplasm of the nearest archegonium.

One of the sperm nuclei migrates through the cytoplasm to the egg nucleus and fuses with it.



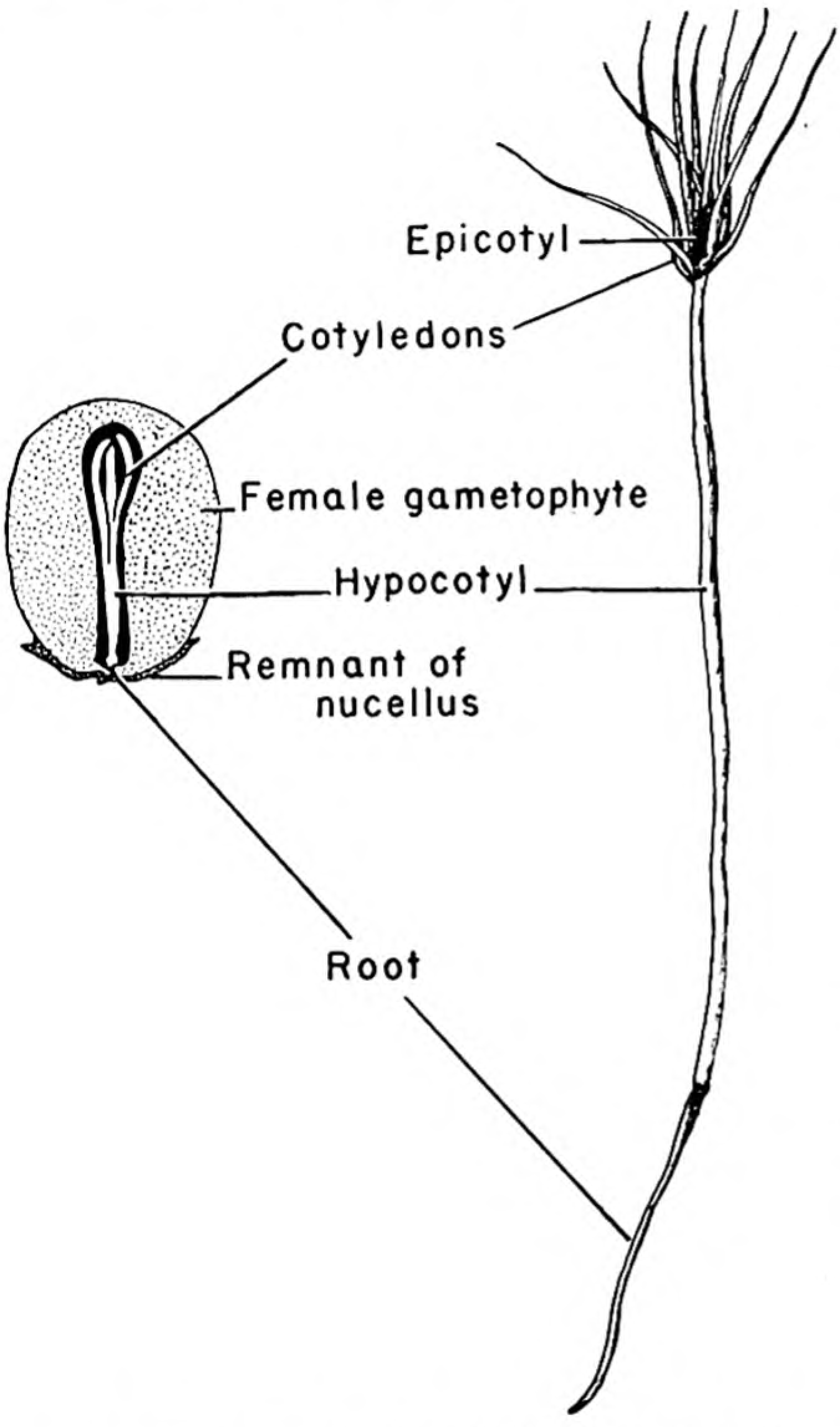
Development of embryos of pine. (A) Early stage in formation of proembryo. (B) Suspensor cells beginning to elongate. (C) The four embryos beginning to organize at end of suspensor.

This is *fertilization*. The other male nucleus disintegrates. In the pines each gamete has 12 chromosomes; the zygote, therefore, has 24. In other words, every cell of the sporophyte of a pine tree has 12 pairs.

THE EMBRYO. The zygote begins to grow at once. Two free nuclear divisions occur and the four resulting nuclei settle to the bottom of the archegonium. Subsequent divisions accompanied by wall formation give rise to a little mass of 16 cells arranged in four vertical columns. This structure is called the *proembryo*.

At this point a peculiar and unusual turn of events sets in. Instead of forming a single embryo, one begins to organize from the deepest cell of each of the four columns. The cells next above elongate, forming *suspensors*, that is, structures that force the young, growing sporophytes deep into the tissues of the female gametophyte. After a time the remaining cells of the proembryo atrophy and disappear and only the embryo and suspensor remain.

The four embryos that develop from a given zygote grow at different rates. In this way one of them usually takes the lead and the other three fail to continue their development.

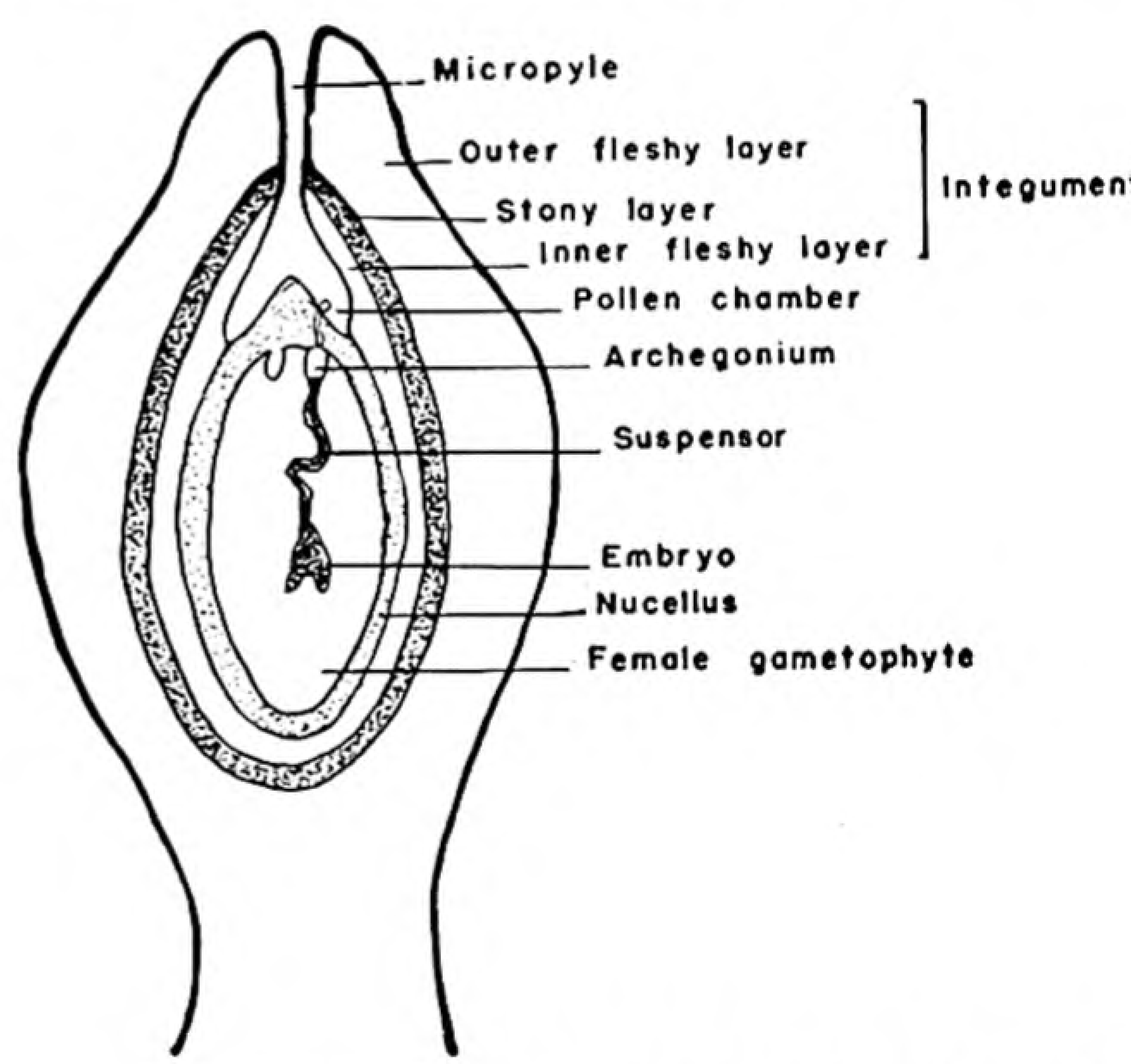


Mature embryo of pine. (*Left*) Seed with testa removed. (*Right*) Seedling.

THE SEED. When the functional sporophyte takes form, it develops four sets of embryonic organs. These are the *hypocotyl* on whose lower end an *embryonic root* becomes organized and on whose upper end is attached the *epicotyl* and from 3 to 12 *cotyledons*, depending on the species of pine. The epicotyl, which is really the embryonic stem, and the embryonic root are little more than apical meristems.

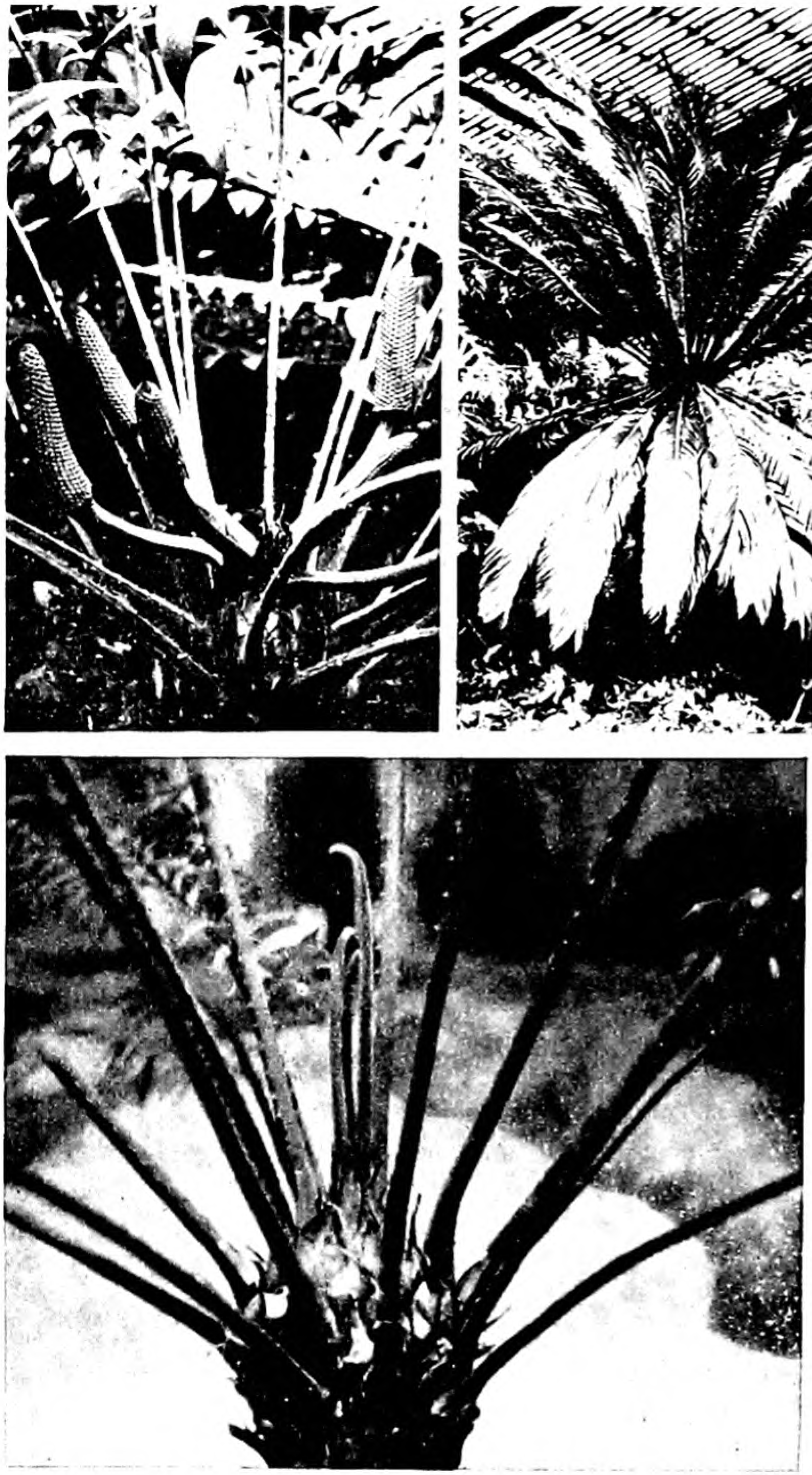
A large part of the female gametophyte, which nourishes the embryo during its development, remains as the *endosperm* of the mature seed; a brown, papery coating over the micropylar end of the female gametophyte is all that is left of the nucellus or megasporangium; and the integument of the ovule becomes the *seed coat* or *testa*. During the latter part of the development of the seed, a broad, flat wing forms on the testa in most species of pine, remaining attached to it, and acting as a sail that causes the seed to be carried some distance by the wind, thus facilitating distribution when the seed leaves the cone.

SUMMARY OF THE LIFE HISTORY. Beginning with a mature sporophyte, that is, a tree, cones make their appearance in early spring. Tetrads of microspores (pollen grains) and megaspores form by meiotic divisions, and pollination takes place within a few weeks. At the end of the growing season the



Diagrammatic longitudinal section through an ovule of a gymnosperm showing the usual structures. Adapted from Sachs.

pollen tube (male gametophyte) has begun to grow in the nucellus, three megaspores have disappeared, and the fourth has begun to organize the female gametophyte in the ovule.



Cycads. (*Top, left*) *Zamia*, staminate cones. (*Top, right*) *Cycas*, plant. (*Bottom*) Young leaves of *Zamia*, showing fernlike circinate vernation.

Early in the following season growth and development are resumed rapidly. Both gametophytes produce gametes. Fertilization occurs, initiating the new sporophyte (embryo) a little more than a year after pollination. The seeds are mature at the end of the second growing season, and fall from the cone during the winter. The mature seed consists of an embryo sporophyte surrounded by a mass of nutritive gametophytic tissue—the endosperm; and this is enclosed in a seed coat coming from the preceding sporophyte generation. Therefore, the seed represents three generations, two being sporophyte and one gametophyte.

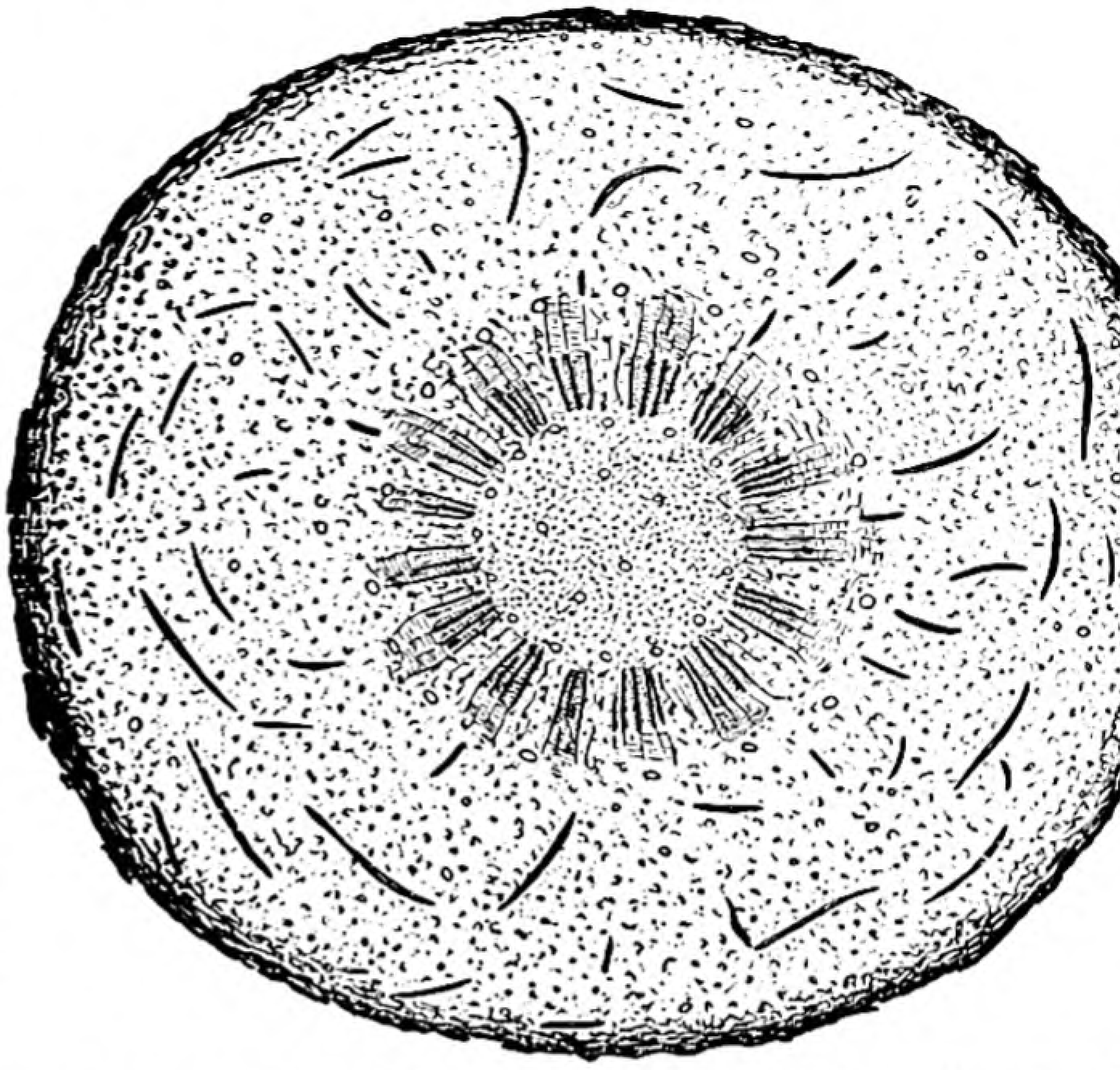
When the seed germinates the food stored in the endosperm is digested and absorbed by the young sporophyte, which eventually grows to be a tree.

Cycadales. The nine genera of gymnosperms which make up the group commonly known as the cycads constitute an inconspicuous part of the present vegetation of the earth, although in Triassic times this order was very important. Most of the genera have only one or a few species, and the number of individuals of any one species is usually not great. These plants are widely but locally distributed in tropical and subtropical regions in both the Eastern and Western Hemispheres. Only one genus, *Zamia*, is native within the continental United States, and it is limited to the state of Florida. Various species belonging to this genus and to the genus *Cycas* from the Orient are frequently grown in greenhouses in this country. All the cycads have much more of the appearance of palms, to which they are not closely related, than to their relatives, the other orders of gymnosperms. The leaves of all are pinnately compound and are usually very hard, stiff, wax-coated and polished, often remaining attached to the trunk for long periods of time, even after they are dead.

This is the most primitive order of all the living seed plants. In fact, the cycads have several characteristics that link them to the ferns rather than to modern seed plants. The leaves have circinate vernation; the sperms are motile by means of numerous flagella, although they have no place in which to swim except within the narrow confines of the pollen tube; and the microsporangia sometimes occur in sori on the lower surface of the microsporophylls.

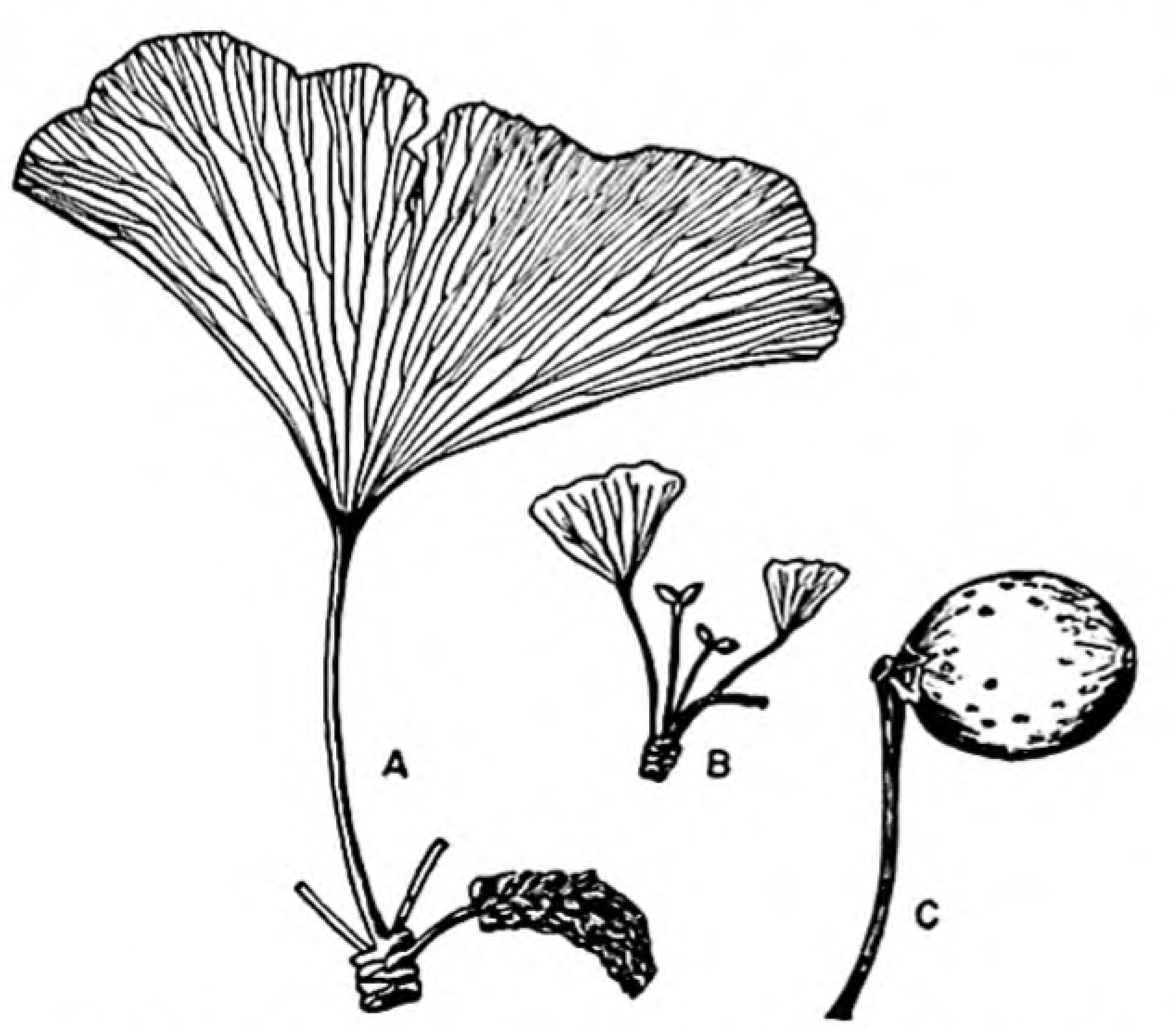
Some of the cycads are small, thick-stemmed perennials and others are tall trees, but all have in common a large central pith and a thick cortex with only a relatively narrow zone of wood. The cambium, however, is somewhat active, gradually adding to the thickness of the xylem.

In *Zamia* each scale of the ovulate cone bears two ovules. As in pine, the pollen is carried by the wind. The development of the gametophytes follows much the same pattern, and fertilization is similar, with the notable exception that the sperms have numerous flagella in *Zamia*, while in pine they have none.



Stem section of the cycad, *Zamia floridana* showing large central pith, thick cortex with numerous curved leaf traces, and narrow zone of xylem and phloem. (Courtesy, Coulter, Barnes, and Cowles: "A Textbook of Botany," Vol. One, New York, American Book Co.)

The seeds are very large, usually falling in a pile near the plant which produces them, and the resulting seedlings are so numerous and so close together that only a small proportion of them survive.

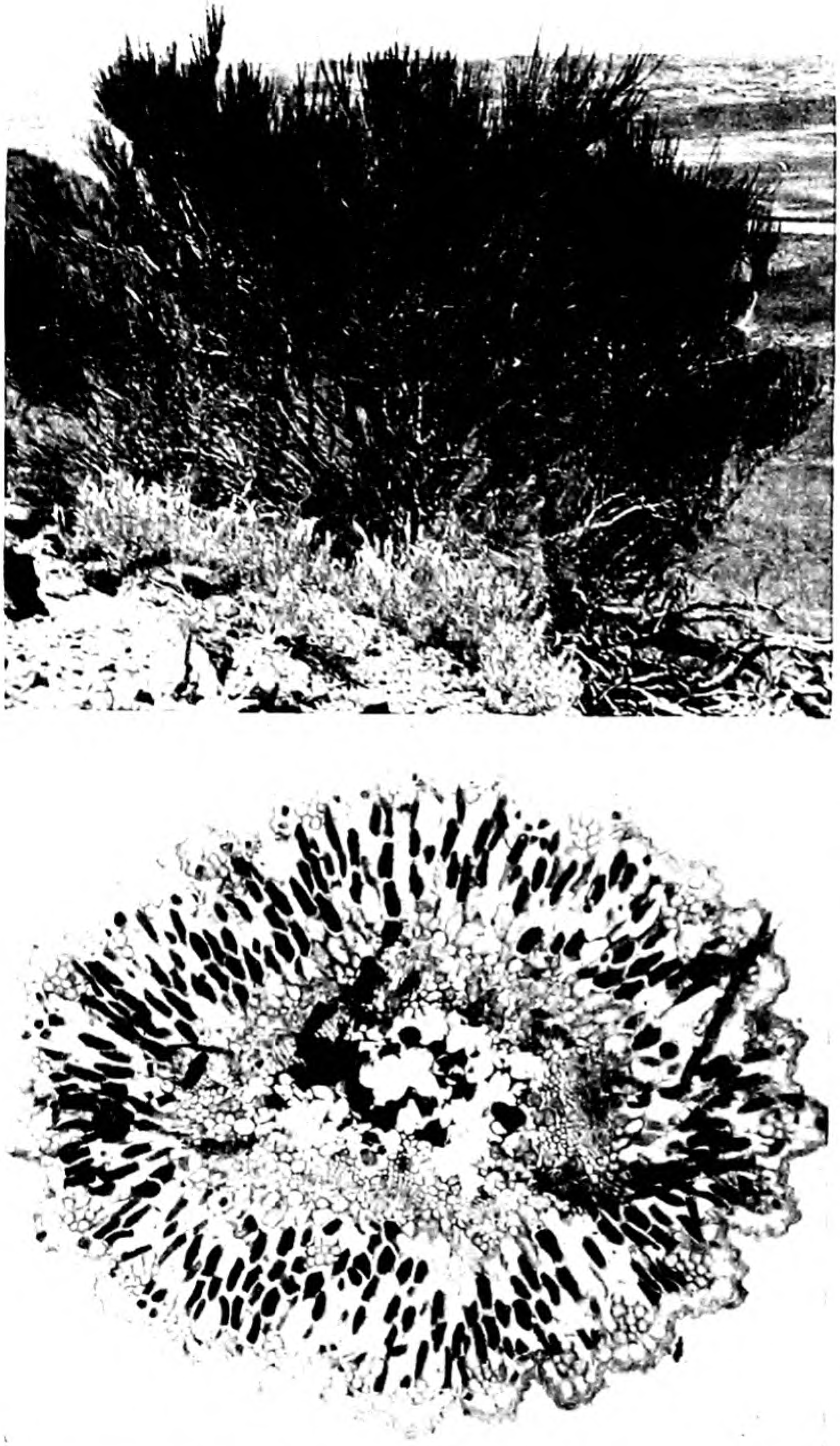


Ginkgo. (A) Twig with leaf and cluster of stamens. Note dichotomous venation in leaf. (B) Twig with ovules and young leaves. (C) Almost mature seed.

Ginkgoales. This order is represented by only one living species, *Ginkgo biloba*. This species is said to have been protected as a sacred tree on temple grounds of the Far East from the times of the earliest records, and during relatively recent years it has been introduced as a successful ornamental in many parts of the world.

The leaves of the ginkgo tree are remarkable because of their dichotomous veining, reminiscent of that of the ferns. In one other way these plants have retained the ancient fernlike characteristics from earlier geologic times: They have swimming sperms. In fact, some paleobotanists are of the opinion that they were derived from the *Cycadofilicales* at about the end of the Paleozoic Era.

No modern gymnosperms other than the cycads and ginkgo have this primitive feature. In these plants, the fine display of flagella appear to serve no useful function because the sperms have no place in which to swim except in a microscopic



Ephedra. (*Top*) Mature plant in desert of northern Arizona. (*Bottom*) Cross section of stem, showing cortex made up of palisade tissue.

bit of cytoplasm within the pollen tube. When it opens, the sperms are forced out into the immediate vicinity of the archegonia, and fertilization takes place much as in pine.

Ginkgo trees are strictly dioecious. Seeds, therefore, are seldom produced unless staminate trees are near the ovulate individuals, thus permitting pollination to take place. The stamens form in small clusters among the young leaves and the ovules grow in pairs fully exposed to the elements at the outer ends of short stalks. Pollination, fertilization and the formation of the seed take place as in the cycads.

As the seed matures the integument ripens in two layers. The outer part becomes the fleshy layer and the inner, which lies in direct contact with the nucellus, changes into a stony layer.

Although the mature seed resembles an orange-yellow plum, it should be clearly understood that it is entirely different in both origin and structure. A plum develops from the ovary of a flower and only the kernel inside the stone comes from an ovule and is a seed. In ginkgo, on the other hand, the entire fruitlike structure develops entirely from an ovule and is, therefore, a seed. This order of plants was at one time almost worldwide, and represented by several genera and numerous species. About 1,000,000 years ago the order all disappeared with the exception of the one species described above.

Gnetales. The three genera, *Ephedra*, *Welwitschia*, and *Gnetum*, which make up the order Gnetales, seem superficially to be very slightly related to each other. Botanists, however, consider them to be rather remotely related because of certain similarities in their anatomy and methods of reproduction. Of these, only one, *Ephedra*, is to be found in the continental United States. This shrubby plant is rather common in the warmer, dryer parts of the Southwest. The various species

take the form of greenish, branched, jointed switches. The leaves are represented by dry, hard scales at each node and photosynthesis is carried on in the cortex of the twigs. In fact the cortex is made up largely of palisades and the epidermis is well supplied with stomata.

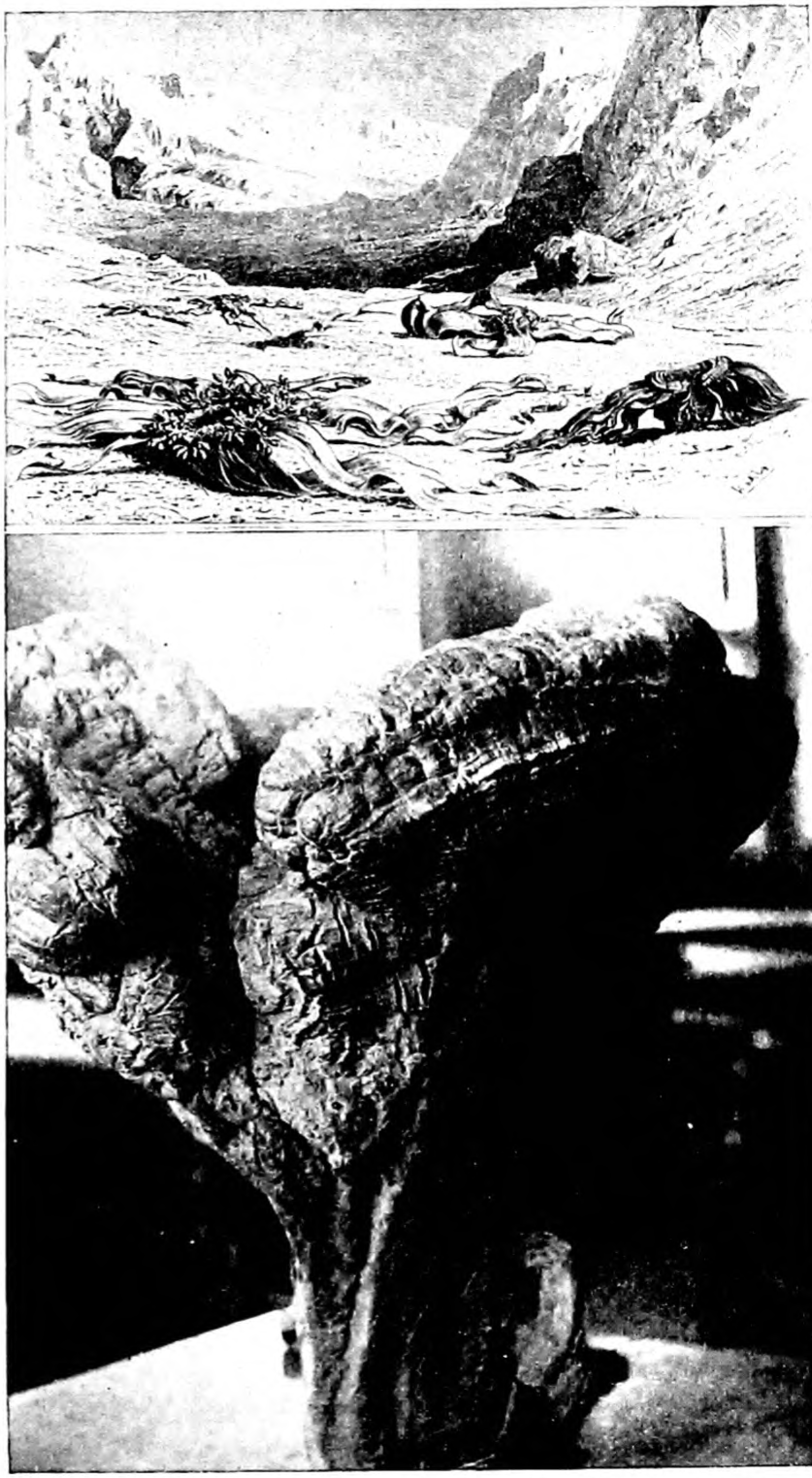
The genus *Welwitschia* is represented by a single species in South Africa. This plant has been described as a "gigantic wooden radish" with a single pair of long leathery leaves that continue to grow and sprawl over the ground during the entire lifetime of the plant.

The remaining genus of this remarkable order is *Gnetum*. All the various species are limited to the tropics. The plants are woody vines and small trees and have the general appearance of dicotyledons with leaves that grow opposite on the stem and have netted veins.

The xylem of all gymnosperms, with the single exception of the members of this order, is made entirely of tracheids, which are one-celled conductive tubes. The Gnetales, in common with the angiosperms, have multicellular vessels in addition to the tracheids.

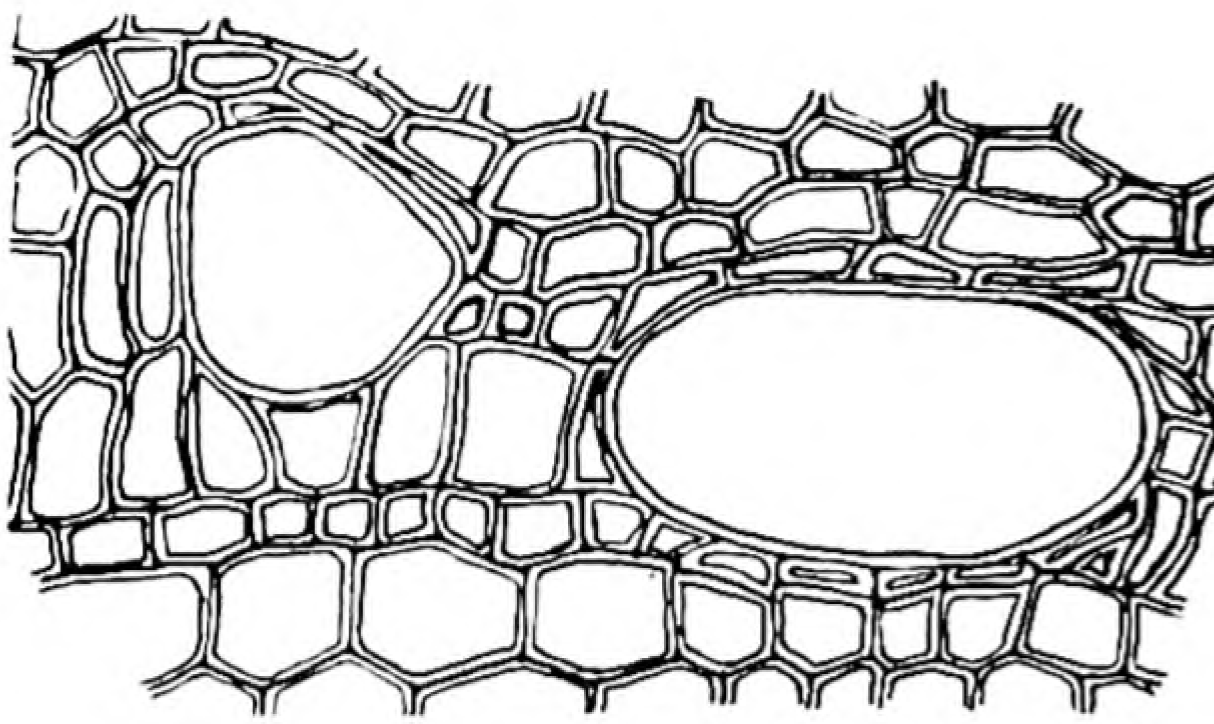
ANCIENT GYMNOSPERMS

The earliest ancestral forms of modern gymnosperms seem to have appeared first in late Devonian times. For many years, students of these fossils failed to recognize them as seed plants but considered them to be ordinary ferns. Finally, seeds were found attached to some of the leaves and it became clear that these were actually seed plants. More recent studies have shown that a vast majority of those ancient leaf



Welwitschia. (*Top*) General view of plants (from Kerner and Oliver). (*Bottom*) Side view of root and stem. Note at widest part at right, the frayed base of one of the wide straplike leaves.

impressions were produced by seed-ferns. Later evolution brought into being other lines of gymnosperms, probably originating from this ancient stock.

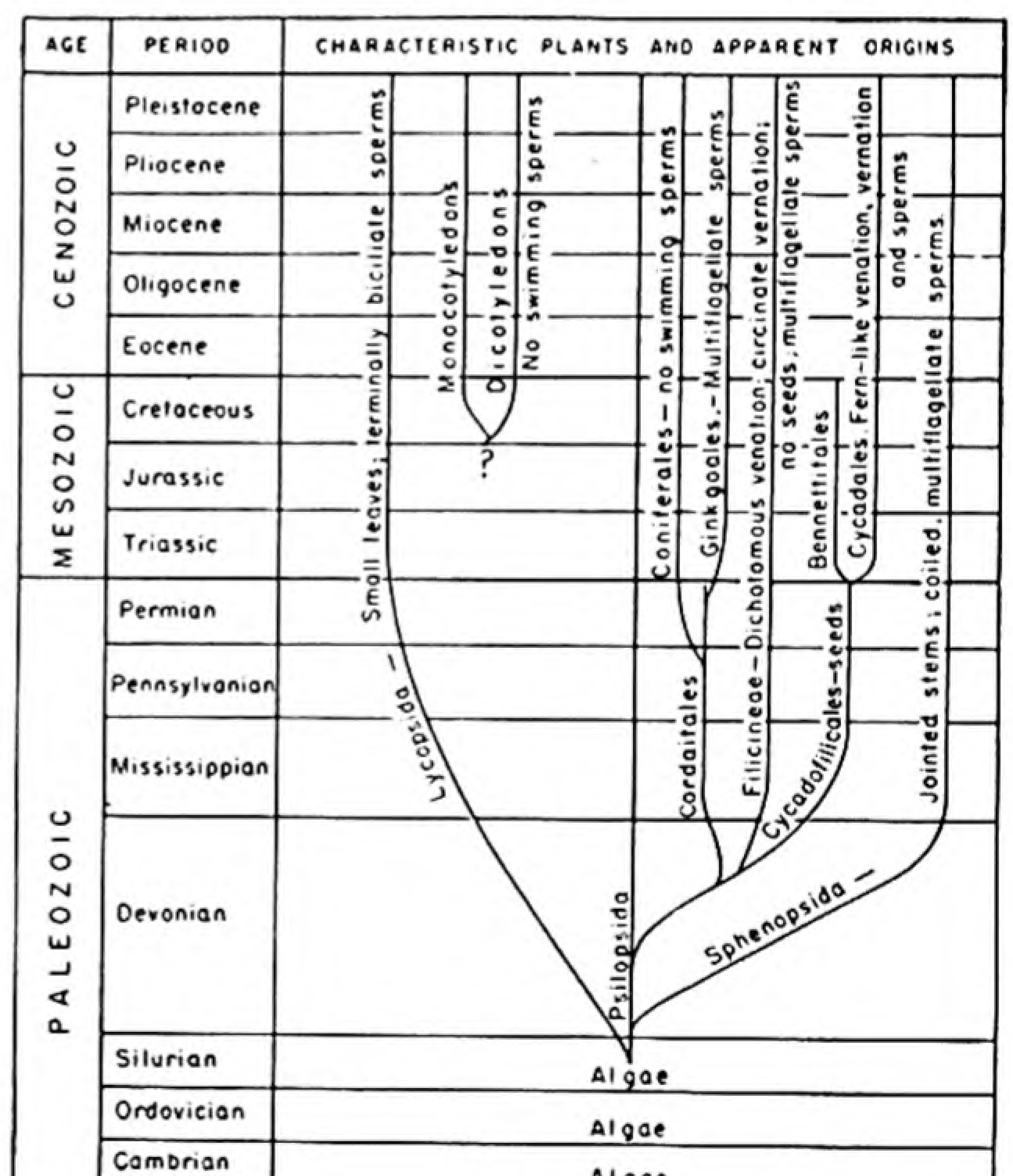


A few cells from the xylem of *Gnetum*. Two large water tubes are crowded in among the numerous tracheids.

Cycadofilicales. The name *Cycadofilicales* was given to this primitive order because these plants had a combination of cycadlike seeds and fernlike vegetative bodies. The seeds, attached to the margins of the fernlike leaves, were somewhat similar in general structure to those of *Ginkgo* and modern cycads, but averaged about the size of a pine seed or an unpopped grain of popcorn. For some unexplained reason, no embryo has yet been discovered within the female gametophyte. All four forms are sufficiently alike to make a definite gymnosperm pattern. The earliest known records came from the strata of the upper Devonian period and they appear to have reached their climax of development during Mississippian and Pennsylvanian times. They assumed a great variety of forms, some of them apparently having the general aspect of modern woodland ferns, while others had large trunks 30 or 40 ft. tall, much like present-day tropical tree ferns.

Cordaitales. The Cordaitales were an order of plants which appeared first in Devonian times and which were very abundant in the Mississippian, Pennsylvanian, and Permian Periods but probably became extinct in the early Mesozoic. These were tall trees with trunks much like those of modern conifers. Some interesting details of structure of the stems and leaves have been determined from the fossils and from the prints which they left in rocks. In many respects the Cordaitales strongly suggest an ancestral relationship with both *Ginkgo* and the conifers. Superficially, at least, their leaves were more like those of the conifer genus *Podocarpus* of Asia than like the narrow-leaved pines so well-known on this continent. Some of those ancient strap-shaped leaves ranged in length from a few inches to 3 feet. While their vegetative characteristics were quite different in some respects from those of the Cycadofilicales, their seeds were almost identical with them, thus indicating close kinship. Although the fossils do not quite prove the point, the Cordaitales seem to have descended from the Cycadofilicales.

Bennettitales. Beginning with the Mesozoic Era, which follows the time during which the Cycadofilicales were such a prominent part of the world's flora, two rather similar groups of gymnosperms made their appearance, as indicated by the



Geologic history of Plant Kingdom showing apparent relationships.

fossil record. Both of these groups had many characteristics in common with Cycadofilicales. These were the Bennettitales and the Cycadales. The cycads have persisted to the present time.

Remains of the Bennettitales have been found in many places scattered from coast to coast in the United States, and from Canada to Mexico. In Eurasia they are known to have lived from Scotland to India. Realizing that conditions were probably not very good for fossilization where these plants grew, their abundance and wide distribution are truly remarkable.

Most of the fossil specimens are short, thick, rather tuberous stems, with cycadlike pinnate leaves. The vascular structure is similar to that of the living cycads.

The most striking feature is the group of spore-bearing structures which, together, are called the *strobilus*. It consists of a central conical axis covered with megasporophylls, each bearing an ovule; around this is a whorl of compound microsporophylls; and around the whole is a covering of scaly, leaflike structures. The arrangement of parts in the strobilus is so much like that of the more primitive present-day flowers that some botanists have suggested that the Bennettitales order may be ancestral to the modern angiosperms. Whatever the relation to the angiosperms, there is little doubt that the cycads have been derived from this group, and that the Bennettitales come from the Cycadofilicales.

Relationships among Gymnosperms. The most ancient of the gymnosperms seem to have been members of the Cycadofilicales. Just what was their origin is not known, for there is not a sufficiently complete fossil record to bridge the gaps between them and their ancestors. The most plausible theory appears to be that they descended, directly or indirectly, from some ancient branch of the Psilopsida. Possibly they evolved along lines parallel with the Filicineae, developing seeds while the true ferns did not; or certain of the ferns may have become heterosporous and produced seeds, in this way giving rise to this cycadofil group.

Out of the Cycadofilicales there almost certainly appeared two great lines of descent. These have been called the cycadophyte and coniferophyte lines. The Bennettitales are at the base of the cycadophytes and the modern cycads constitute the apex. Likewise, the Cordaitales—those tall slender trees—seem to have given rise to the conifers, the Ginkgoales, and possibly the Gnetales.

SUPPLEMENTARY READINGS

Andrews, "Ancient Plants and the World They Lived In."
Arnold, "An Introduction to Paleobotany."
Berry, "Tree Ancestors."
Darrah, "Textbook of Paleobotany."
Eames, "Morphology of Vascular Plants."
Eames and MacDaniels, "An Introduction to Plant Anatomy."

Chapter 21

PTEROPSIDA: ANGIOSPERMAE

Angiosperms are the plants whose ovules and developing seeds are wrapped in protective coverings—the ovary walls. These are the plants that are pioneering in the world today and with which mankind is most familiar.

Here the last trace of the archegonium and the swimming sperm, with their limitations, are gone. Instead, the sperm nucleus is transferred directly to the egg nucleus through a pollen tube within the style. All this reproductive activity is carried on by the agency of that peculiarly angiosperm structure, the flower, with which this chapter is introduced. The remainder of the chapter traces the story of this class of plants as outlined below.

The present is the age of the angiosperms. Although they did not take their place among the great plant groups until relatively recent geologic times, they have extended their range from the tropics to the arctic regions and from far above timber line in the mountains down to sea level. A few can live in shallow water in lakes, ponds, and streams, and along the ocean coasts. Some thrive in the deserts and others are limited to swamplands. In fact, angiosperms are so familiar that many people are only vaguely aware that there are any other kinds of plants. Even cultivated crops are almost without exception members of this, the highest, expression of plant life.

The earlier chapters of this book, dealing with the general functions and structure of leaves, roots, and stems, were based largely upon examples selected from among the angiosperms. It is therefore not necessary to repeat the description of their vegetative forms.

The Flower. The most outstanding and distinctive characteristics of modern angiosperms are the various parts of the flower. In some instances this is a very simple, unattractive object; in others it is remarkable for its complexity. So far as the plant is concerned, however, the flower is important because it acts as an agency that brings about the transfer of pollen from anther to stigma and the

consequent fertilization of the egg and production of the zygote. The accompanying diagram shows the relative positions of the parts of a very simple flower.

The buds and open flowers of such well-known plants as strawberry, wild geranium, or bluebell are suitable to illustrate a common type of floral structure. The outermost covering of an unopened bud of one of these plants is made up of five green *sepals*. All the sepals taken together as a unit constitute the *calyx*. In a flower that is just beginning to open there are to be seen five white, pink, or blue *petals* attached in a circle just inside the sepals. Considered as a unit, the petals constitute the *corolla*, and calyx and corolla together are often called the *perianth*.

The perianth has no direct part in the processes of pollination but has the dual role of protecting the delicate inner organs while they are in the bud and, later, of attracting insects that carry the pollen.

When the flower is fully open numerous stamens are revealed, forming a circle just inside the ring of petals; occupying the center is a group of *carpels*. All these parts—calyx, corolla, stamens, and carpels —are attached to the *receptacle*, the somewhat specialized summit of the *pedicel*. The stamens and carpels are the functional parts that are directly concerned with the production of seeds.

Each stamen is composed of a slender thread, the *filament*, topped by a pollen-bearing enlargement, the *anther*. Likewise, a carpel is composed of a receptive *stigma*, an *ovary* containing one or more *ovules*, and a more or less elongated *style* between the ovary and the stigma. The stamens produce pollen grains (microspores) which normally become attached to the stigmas, where they germinate, developing pollen tubes. These pollen tubes are, in effect, male gametophytes in which sperm nuclei are formed. The sperms fertilize the eggs in the ovules, initiating the changes which transform them into mature seeds.

A marked contrast between the behavior of pollen in the gymnosperms and in the angiosperms should be made clear. In all the gymnosperms the pollen grain passes bodily through the micropyle where it develops a short tube that delivers the sperms to an archegonium with its egg. In the angiosperms the ovule with its micropyle is deep in the protective ovary, and the pollen tube must grow from the stigma through the style and to the ovule before its two sperm nuclei can reach the female gametophyte with its egg nucleus.

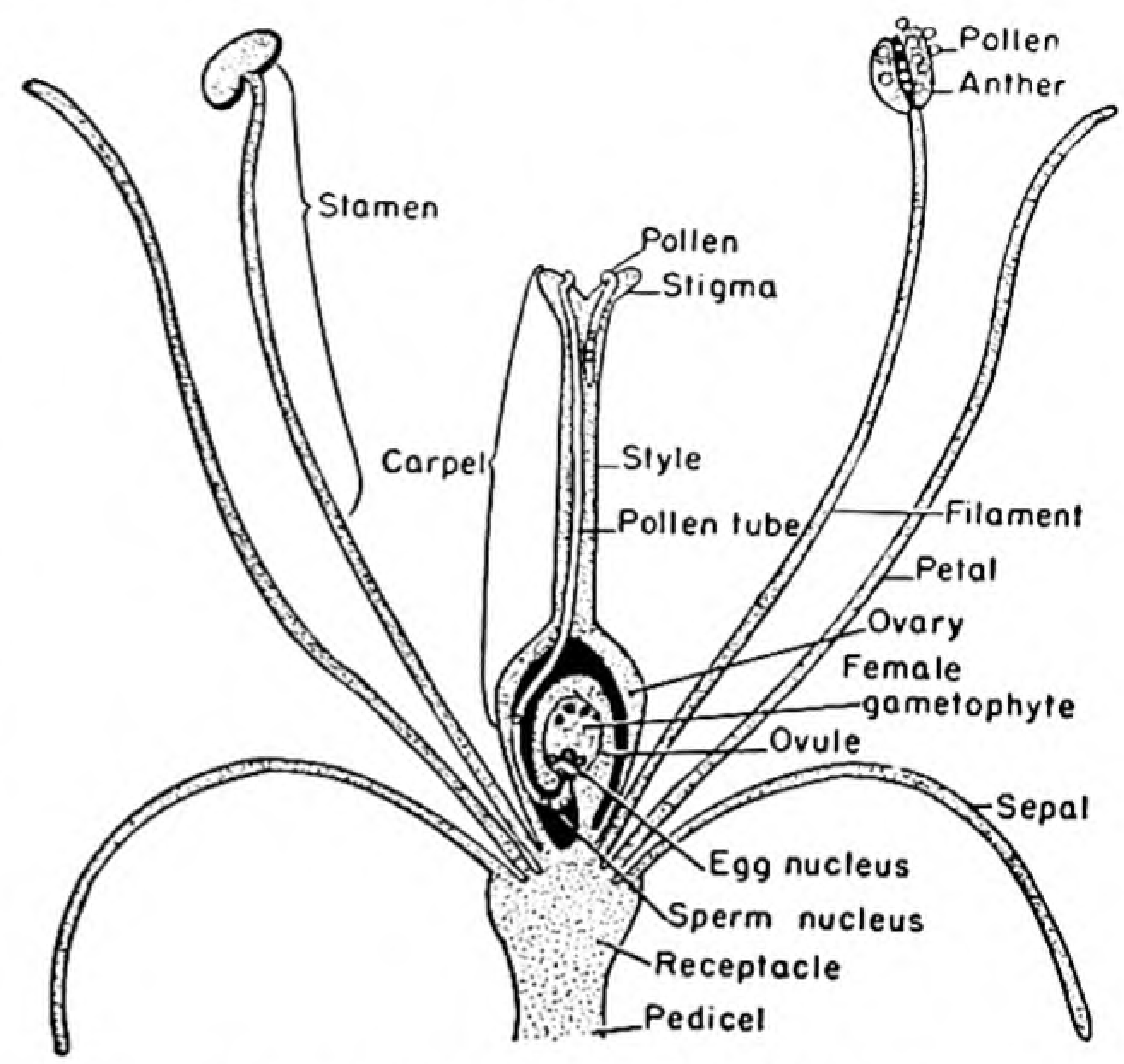


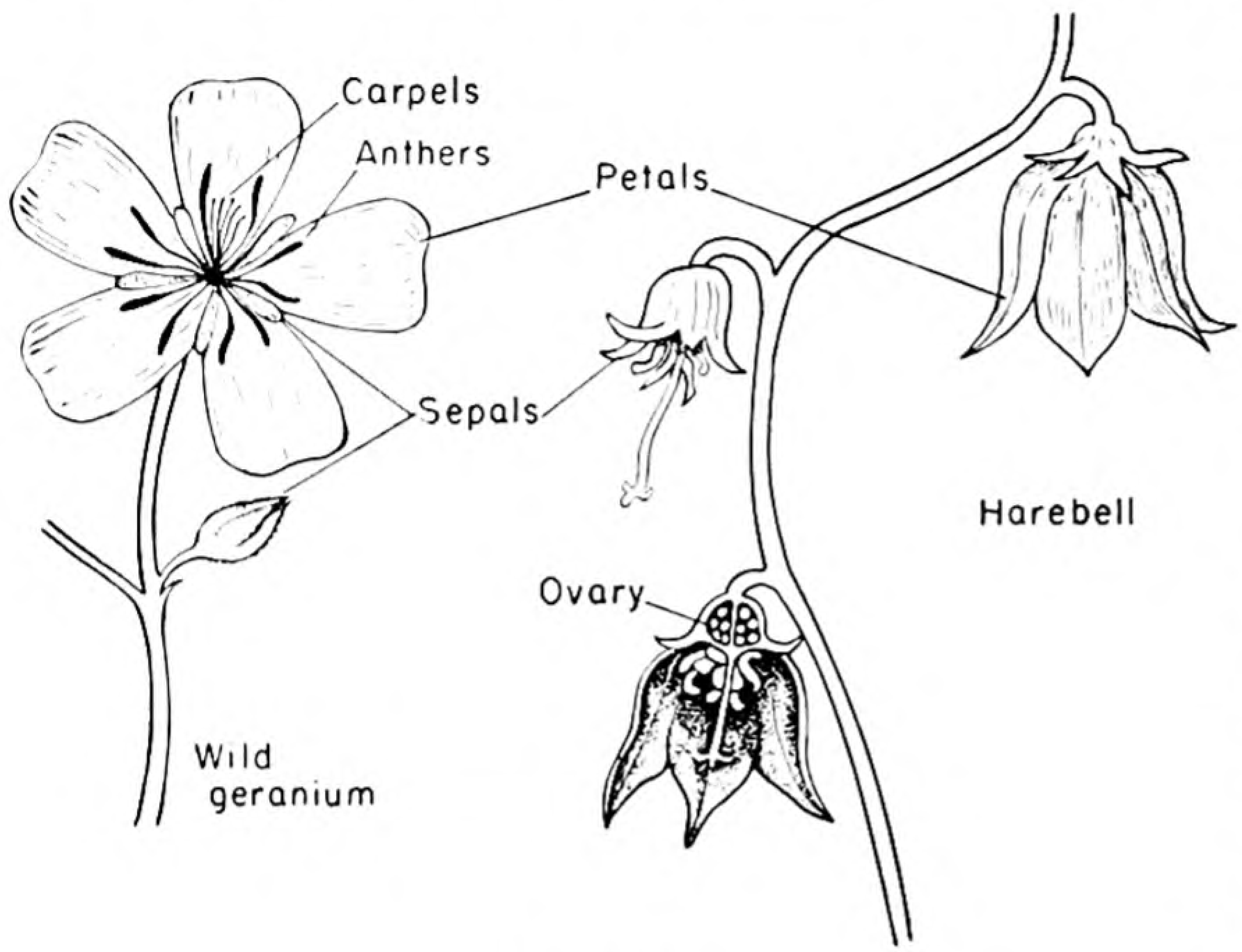
Diagram of a flower showing parts.

The Stamen. The functional part of a stamen is the anther. By cutting cross sections of anthers it is possible to follow the development of the pollen grains and surrounding tissues.

While the anther is still young, masses of pollen mother-cells become differentiated in each microsporangium. Between these cell masses and the sporangium wall there organizes a specialized nutritive cellular layer, the *tapetum*. The tapetum cells disorganize, supplying the nourishment that is used in the development of the pollen mother-cells. Each of these undergoes meiotic divisions and produces a tetrad of pollen grains or microspores. The partitions break down between adjacent microsporangia. As a result, the mature anther usually consists of two thin-walled cavities. These cavities burst open in various ways and release the pollen.

When the pollen grain is formed it consists of a single haploid cell. Almost universally it begins to germinate before it leaves the anther. In other words, it begins to form the male gametophyte. The initial steps of germination recall those of the

microspores of *Selaginella;* that is, they occur and the male gametophyte organizes wholly inside the spore wall. The microspore nucleus divides mitotically, into the *generative* and *tube nuclei*. The former next divides, making two *sperm nuclei*. At this stage the male gametophyte is mature. In some species the pollen is not shed until this stage is reached.



Parts of flower.

POLLINATION. The transfer of pollen from the anther which produces it to the stigma on which it is to become effective is known as *pollination*. It will be recalled that in the same process in gymnosperms the pollen grain is carried, not to a stigma, but directly to the micropyle of the ovule.

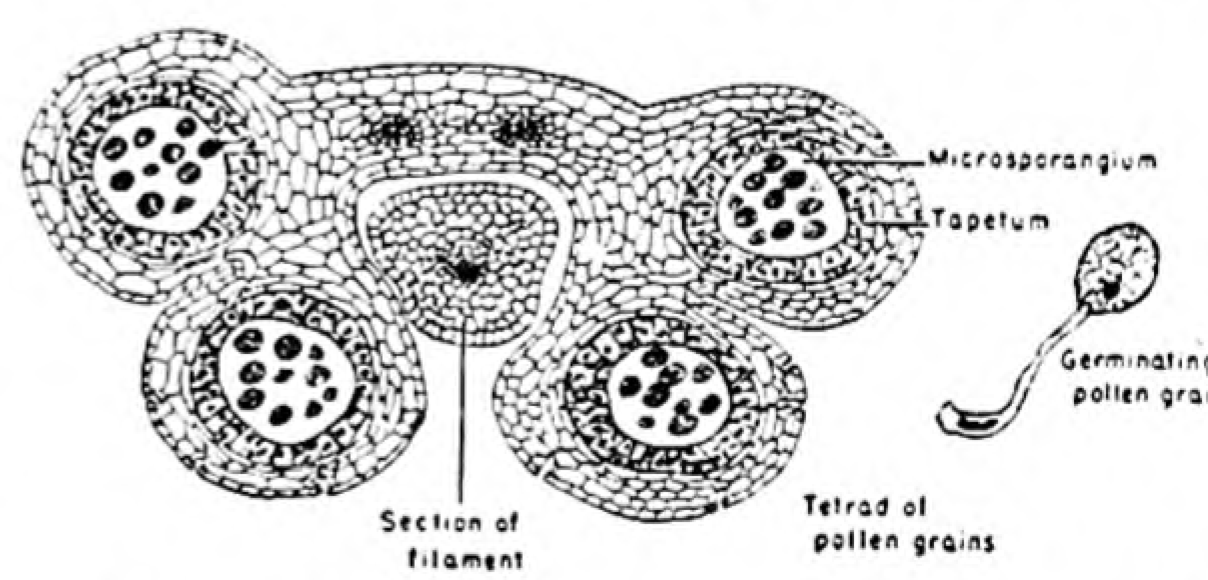
Pollination is accomplished by a number of agencies among which are wind, water, and insects, and there are many correlations between the structure of the flower and the method of transfer of its pollen. A more detailed discussion of these agencies will be given later (see pp. 326–329).

THE POLLEN TUBE. On arriving at its destination on the stigma, the pollen grain resumes growth. Its wall bursts, and the end of a slender, delicate *pollen tube* emerges. It soon penetrates the stigma and grows through a richly nutrient tissue within the style, extending its length toward the ovules. This entire male gametophyte consists of a pollen grain and pollen tube containing cytoplasm and three nuclei, two of which are capable of acting as sperms.

In small flowers the distance from stigma to ovule is usually only a fraction of an inch, but in the large ones of lily or amaryllis it may be several inches. Probably the greatest distance is found in some flowers of very unusual nature, such as those of the corn plant where it is represented by the length of the "silk."

It is not to be understood that in these longest styles a living pollen tube extends at any one time from the stigma to the ovule. As the tube grows at one end it dies at the other, and the living portion is never very long. The time required for the tube to grow from the stigma to the ovule is usually relatively brief. Even in the corn plant, under ordinary conditions, it is probably only three or four days.

CARPEL AND PISTIL. The *carpel* is the unit structure which produces ovules. It is usually made up of an ovary containing at least one ovule, plus a style, and a stigma. In many species, two or more carpels are organized together, making a compound struc-



Microspores and male gametophytes. (*Left*) Cross section through lily anther. (*Right*) Pollen grain germinating and forming pollen tube. Tube nucleus is in lower end of tube; generative nucleus is in pollen grain. Later this nucleus divides and produces the two sperm nuclei.

ture. The term *pistil* is often applied either to the simple or the compound ovule-producing part of a flower. That is to say, a pistil may be simple, composed of one carpel; or compound, made up of more than one. In many instances it is difficult to determine whether a pistil is simple or compound. When there is more than one style or stigma or more than one ovule-containing chamber (commonly called a "cell") in the ovary, the pistil is considered to be compound.

The ovules are attached to the *placentae* within the ovary. A placenta may have the form of a knob, ridge, or conical projection extending inward from the wall of the ovary, or sometimes it may be only a slightly specialized portion of the inner surface of the wall.

The Ovule. An ovule begins its development as a small, rounded protuberance on the placenta. This rounded body is the forerunner of the nucellus. One or two layers, only a few cells thick, grow up from the base of the young ovule, forming the *integuments.* When growth is completed, the integuments entirely cover the nucellus with the exception of a small hole at the outer end. This hole is the *micropyle.* Through it, in most species, the pollen tube later enters the ovule. At the end opposite the micropyle a short, stalklike structure, the *funiculus,* takes form, connecting the ovule to the placenta and through it to the ovary wall. When the ovule develops into a mature seed, the nucellus is largely or wholly replaced by the embryo or by the embryo and endosperm, and the integuments become the seed coat, or *testa.*

THE MEGASPORE. While the ovule is yet young, the megaspore mother-cell is differentiated as a larger, more active cell in the tissue of the nucellus. In earlier times, before the details of gametophyte development and fertilization were understood, it was discovered that the embryo formed in a greatly enlarged cell in the ovule. This cell came to be known as the *embryo sac.* Although less accurate, the expression is so convenient that it is still used, sometimes, to indicate any stage in the development of the female gametophyte. Its manner of origin varies somewhat in different species, but these details may be ignored for the present.

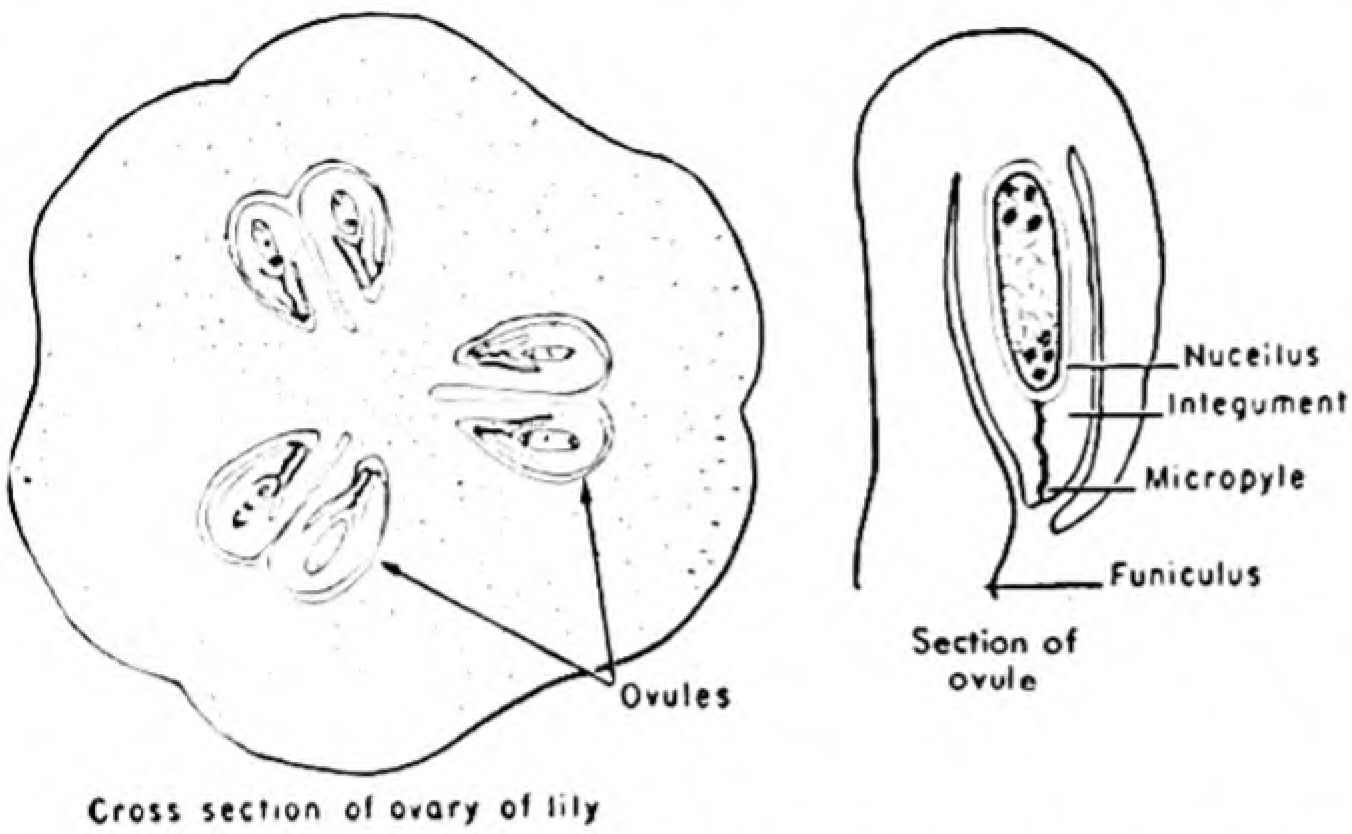
After a period of growth in which the mother-cell enlarges considerably, meiosis occurs and the result is a group of four *megaspores.* As in the gymnosperms, these spores become arranged in a line and the group is called a *linear tetrad.* From this point on there is considerable variation in behavior in different species but what seems to be the common line of action will be outlined here.

THE COMMON TYPE OF FEMALE GAMETOPHYTE. In many of the angiosperms three of the megaspores are absorbed by the fourth, which is usually the one most distant from the micropyle and therefore is nearest to the attachment of the ovule to the funiculus. The point of attachment is called the *chalaza.*

Corn at pollination time. The long, slender silks are the styles of the flowers, one silk connecting with each grain.

This megaspore enlarges rapidly, and three consecutive nuclear divisions result in eight free nuclei, that is, nuclei that are not surrounded by cell walls, but that float freely in the cytoplasm. This development may be regarded as the germination of the megaspore in forming a female gametophyte. At the chalazal end of the gametophyte three of the

nuclei are sometimes cut off by plasma membranes, making the *antipodal cells*. Although they are frequently very large and conspicuous, they probably have no important function. At the micropylar end



Ovary and ovules. (*Left*) Ovary of lily as seen in semidiagrammatic cross section, showing three cells, each with two ovules. (*Right*) Ovule showing female gametophyte with eight nuclei surrounded by nucellus. Two integuments enclose the nucellus and fail to close completely, leaving the micropyle. The stalk that attaches ovule to placenta is the funiculus.

of the embryo sac, cells are formed involving three more of the nuclei. One of these is the egg; the other two are known as *synergid cells*.

Of the original eight nuclei the two remaining, called the *polar nuclei*, come together near the center of the female gametophyte. In some species they fuse and in others they remain distinct but near together. Since they are to play a part in the formation of the endosperm of the seed, they are often referred to as the *endosperm nuclei*.

This peculiar seven-celled structure is the mature *female gametophyte*. Being a gametophyte, it has completed its function in the life cycle by producing an egg, and no further development can occur without union with another gamete.

FERTILIZATION. In the meantime, if normal pollination has taken place, a pollen tube has been growing toward the ovule, digesting its way through the nutritive tissues of the style. It may have followed any one of several routes, but in most plants it enters by way of the micropyle and penetrates any portion of the nucellus which may block its way. Its tip elongates a short distance into the female gametophyte. Then it breaks open. High osmotic pressure within the pollen tube drives the two sperm nuclei out near the egg nucleus.

Soon after the contents of the pollen tube have been emptied into the embryo sac, one of its two sperms unites with the egg, producing the zygote, the cell which will develop into the embryo of the seed. In a great many of the plants which have been examined for this feature the other sperm unites with the polar nuclei, giving rise to the cell from which the endosperm is to develop.

This "double fertilization," that is, the fertilization of both the egg and the endosperm cell, has been the subject of a great deal of study and controversy since it was discovered in 1900. At first, many thought that the fusion of nuclei in the endosperm cell occurred in only a few plants and was not worthy of much consideration, while others thought that it should not be regarded as a true fertilization. It is now generally admitted, however, that the double fusion is of common occurrence, probably taking place in a majority of the angiosperms, and that in such plants the endosperm has a true sexual origin.

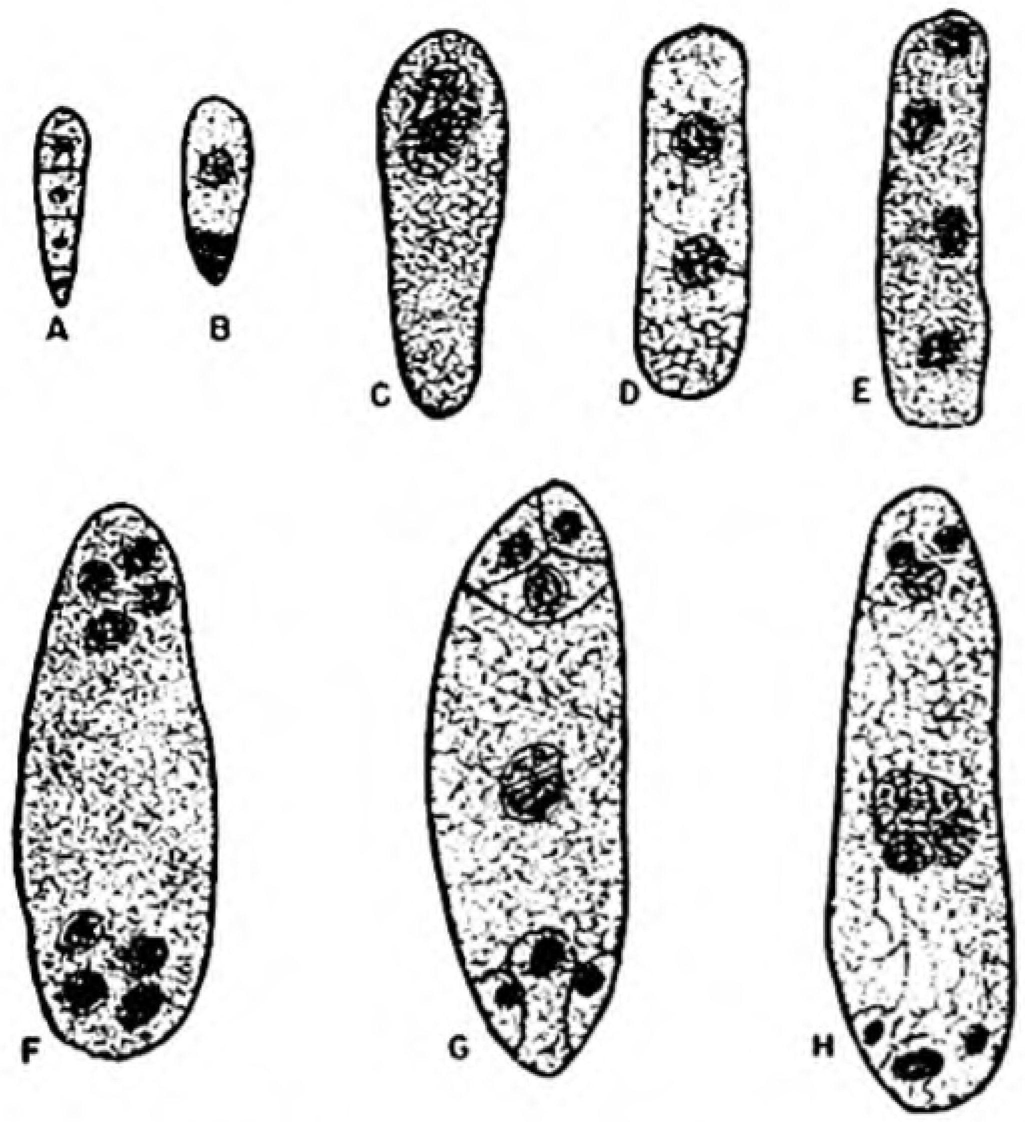
Whereas each cell of the embryo contains $2n$ chromosomes, those resulting from the triple fusion contain $3n$ chromosomes, $2n$ from the female gametophyte and n from the male nucleus. How does this endosperm compare with that of pine?

In a considerable number of angiosperms, however, the two nuclei of the endosperm cell have united to form a fusion nucleus before the arrival of the pollen tube, and the second sperm may not unite with it. In such instances there is no double fertilization, but the endosperm is a diploid structure because of the two nuclei of the female gametophyte which united to initiate its development. In many species the endosperm forms a considerable mass of nutritive tissue around the embryo, while in others it fails to develop and in still others it forms and then is absorbed by the growing embryo. In any case it is a poorly organized tissue which does not reproduce itself.

OTHER TYPES OF FEMALE GAMETOPHYTE. Although most angiosperms which have been studied

have the seven-celled female gametophyte just described, there are a number of other types which deserve brief mention.

Some of these represent a reduced condition in



Usual type of development of female gametophyte of angiosperm and the process of fertilization. (A) Linear tetrad of megaspores. (B) Three of the megaspores being replaced by the fourth. (C) Mature megaspore. (D, E, F) Two, four, and eight nuclear stages in development of female gametophyte. (G) Mature female gametophyte showing the three antipodal cells (*above*), the two polar cells (*center*), the egg with two smaller synergids (*below*). (H) Fertilization, showing one sperm nucleus uniting with the two polar nuclei and the other sperm nucleus uniting with the egg.

which the megaspore produces only four, or even only two cells, one of which is the egg. In others, including the corn plant and many other grasses, the antipodal cells divide and produce a considerable body of vegetative tissue before the time of fertilization.

Lilium is used extensively in laboratory work and since the female gametophyte does not follow the standard series of steps in its development, the following outline will simplify the interpretation of the embryo sac.

The uninucleate stage is the megaspore mother-cell. Meiosis takes place in the usual manner, producing four nuclei of about the same size which are, in effect, megaspores. From this point on development is unusual. One megaspore nucleus migrates to the end nearest the micropyle and the other three move to the chalazal end of the embryo sac. The micropylar nucleus divides mitotically but the three chalazal ones fuse and then divide, forming two giant nuclei. This is called the second four-nucleate stage. One more division produces eight.

After reaching this stage, the embryo sac returns to a normal cycle of development with the formation of the endosperm nucleus and double fertilization. Accompanying is a diagram comparing the standard development of the female gametophyte with that of *Lilium*.

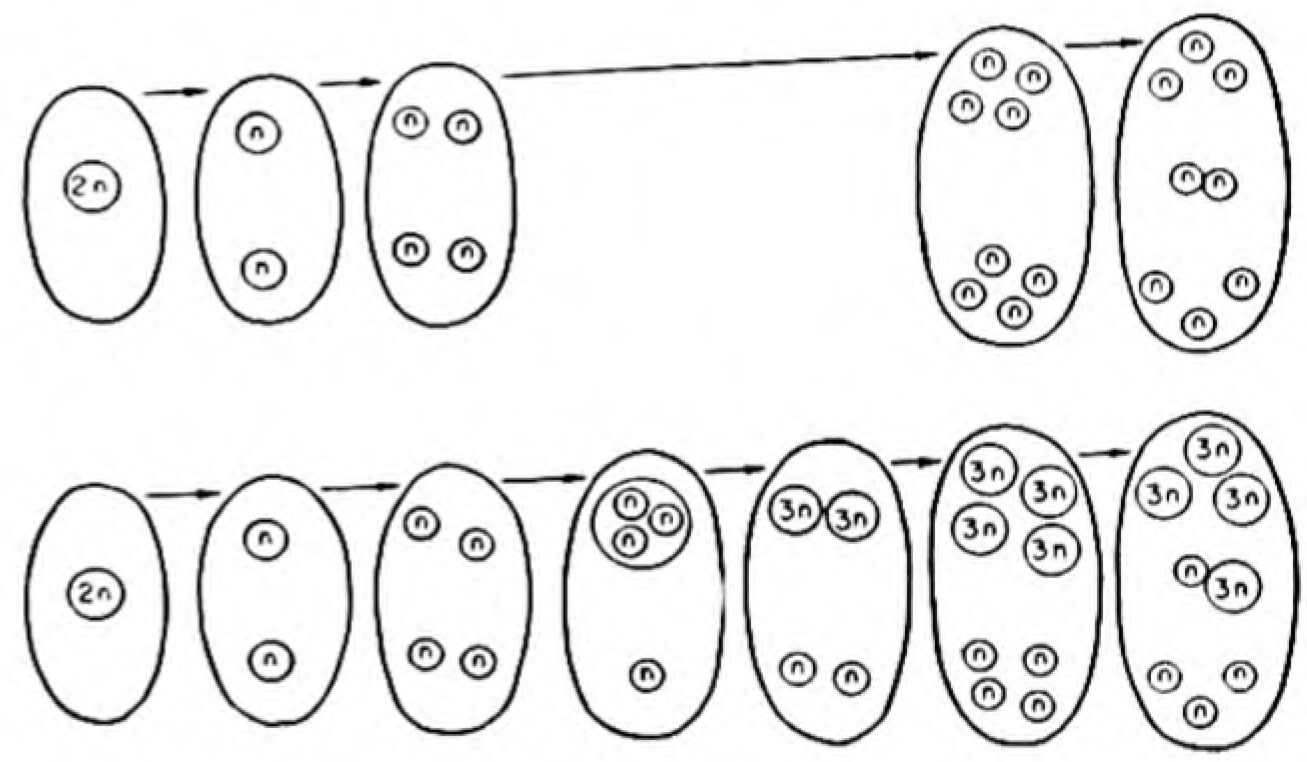
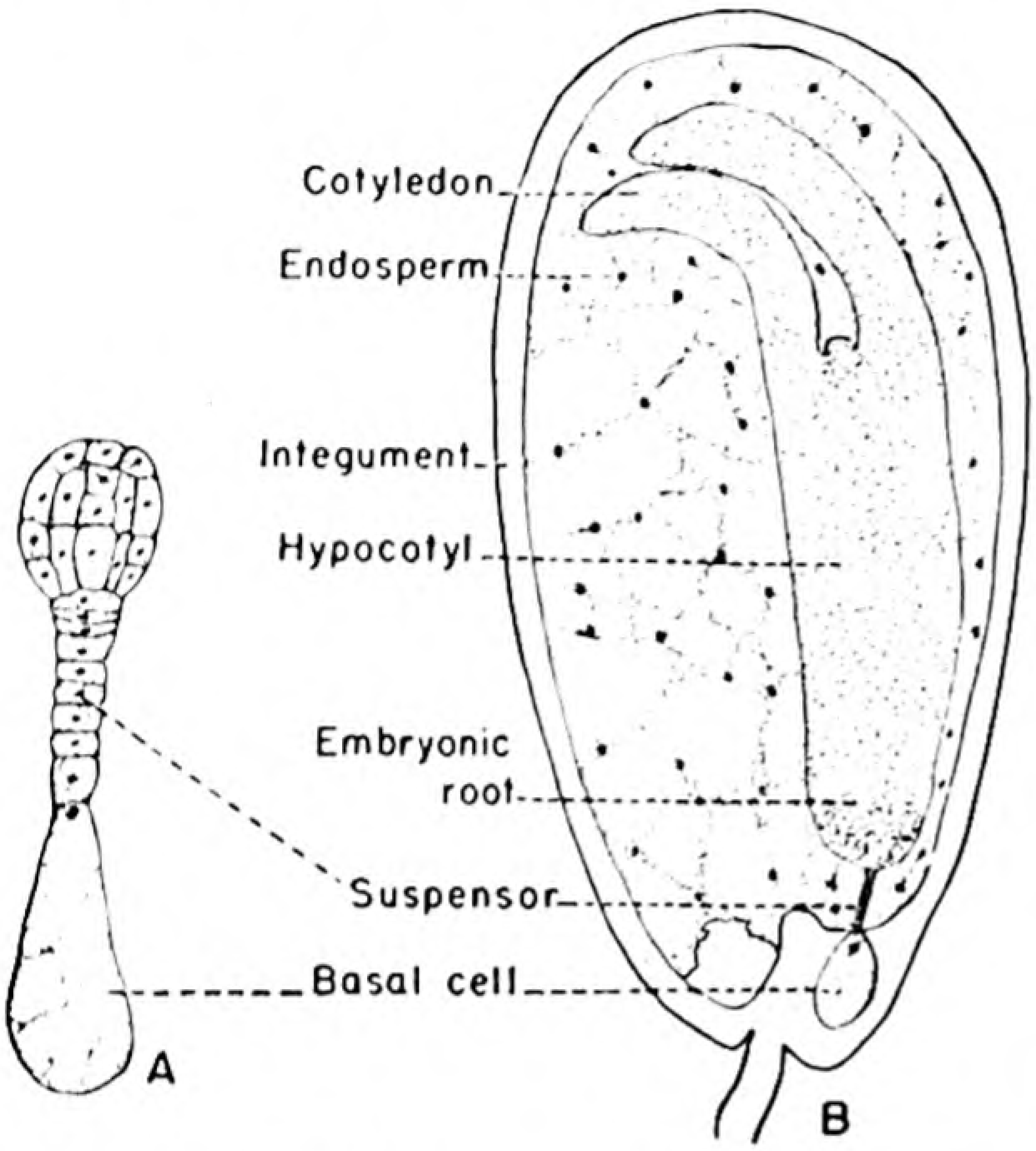


Diagram comparing the development of the more usual type of female gametophyte of angiosperms (*top*) with that of lily (*bottom*).

Development of the Seed. The origins of the various parts of the mature seed have already been indicated. The integument becomes the testa; the fertilized egg produces the embryo; and the endosperm cell, with or without the help of a sperm, gives rise to the specialized nutritive tissue. During early stages of the development of the endosperm, whatever its origin, there is a period of free nuclear division, making a large number of nuclei around the growing embryo. Later, cell walls form around the free nuclei, organizing a tissue which rapidly becomes filled with reserve foods. The developing endosperm destroys all or a part of the nucellus. In some species the growing embryo, in turn, absorbs the endosperm, while in others it does not, in which case the endosperm persists until the seed germinates.

THE EMBRYO. The embryo begins to develop soon after fertilization. In most species it becomes differentiated into two parts, a long, slender, rapidly growing *suspensor* with its greatly enlarged



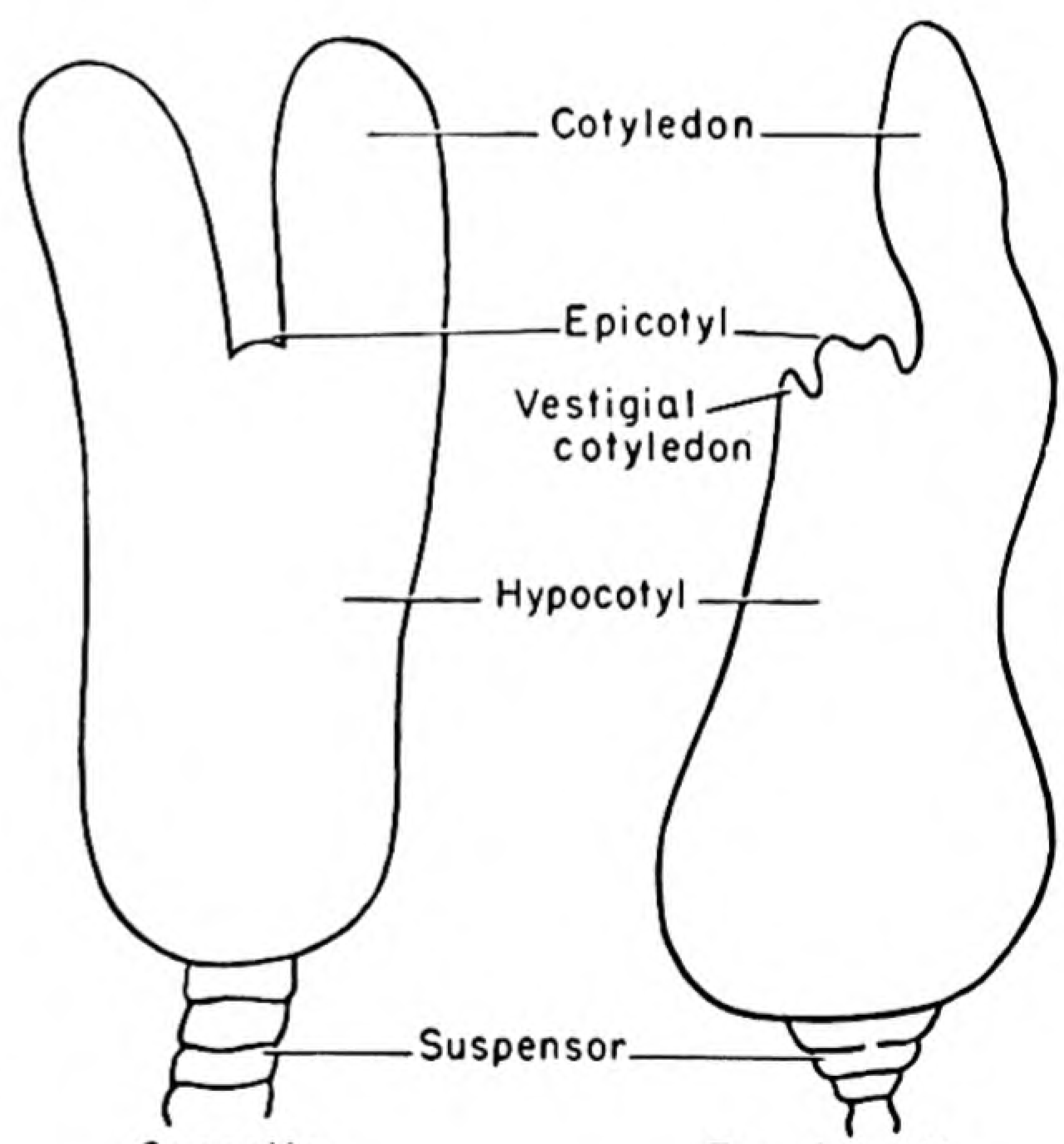
The embryo. (A) Young embryo of *Capsella* with its slender suspensor and large basal cell. (B) Older embryo and other parts of developing seed.

basal cell and, opposite it, a rounded compact mass of tissue which gives rise to the embryo proper. The elongation of the suspensor pushes the body of the embryo into the endosperm. The embryonic tissues soon begin to differentiate, giving rise to two apical meristems, one of which becomes the *embryonic root*, while the other, pointing in the opposite direction, forms the *epicotyl* or embryonic shoot. Between these two and uniting them is the *hypocotyl*. At its summit just below the epicotyl, the one or two *cotyledons* form; one in monocotyledons and two in dicotyledons.

Development of the Fruit. As the seeds of an angiosperm develop following fertilization, the ovary becomes a *fruit*. Botanically speaking, then, *a fruit is a ripened ovary, with or without accessory structures, containing one or more seeds*. From the standpoint of the plant, a peanut shell containing its seeds, or a cocklebur, is as distinctly a fruit as is an apple. Sometimes other parts of the flower closely associated with the ovary, such as the calyx or receptacle, or even a considerable portion of the end of the stem, also enter into the structure of the fruit.

If pollination is prevented, the floral parts usually die, and the ovary shrivels and falls off. The development of the seeds in some plants, and the growth of pollen tubes in others, provides a stimulus, probably from growth hormones, causing the surrounding parts to grow and mature. As a rule, the most perfect fruits are formed when fertilization has occurred in all or nearly all the ovules in the ovary, but in some species fertilization in even a small portion is sufficient.

FRUIT AND SEED. An examination of peanuts in the shell will summarize and clarify the relations of the parts already discussed. The shell is the ovary wall and the edible nuts are the seeds. The brown papery covering of the seed is the testa, the two large halves of the nut are the cotyledons, and the epicotyl, hypocotyl, and embryonic root are very

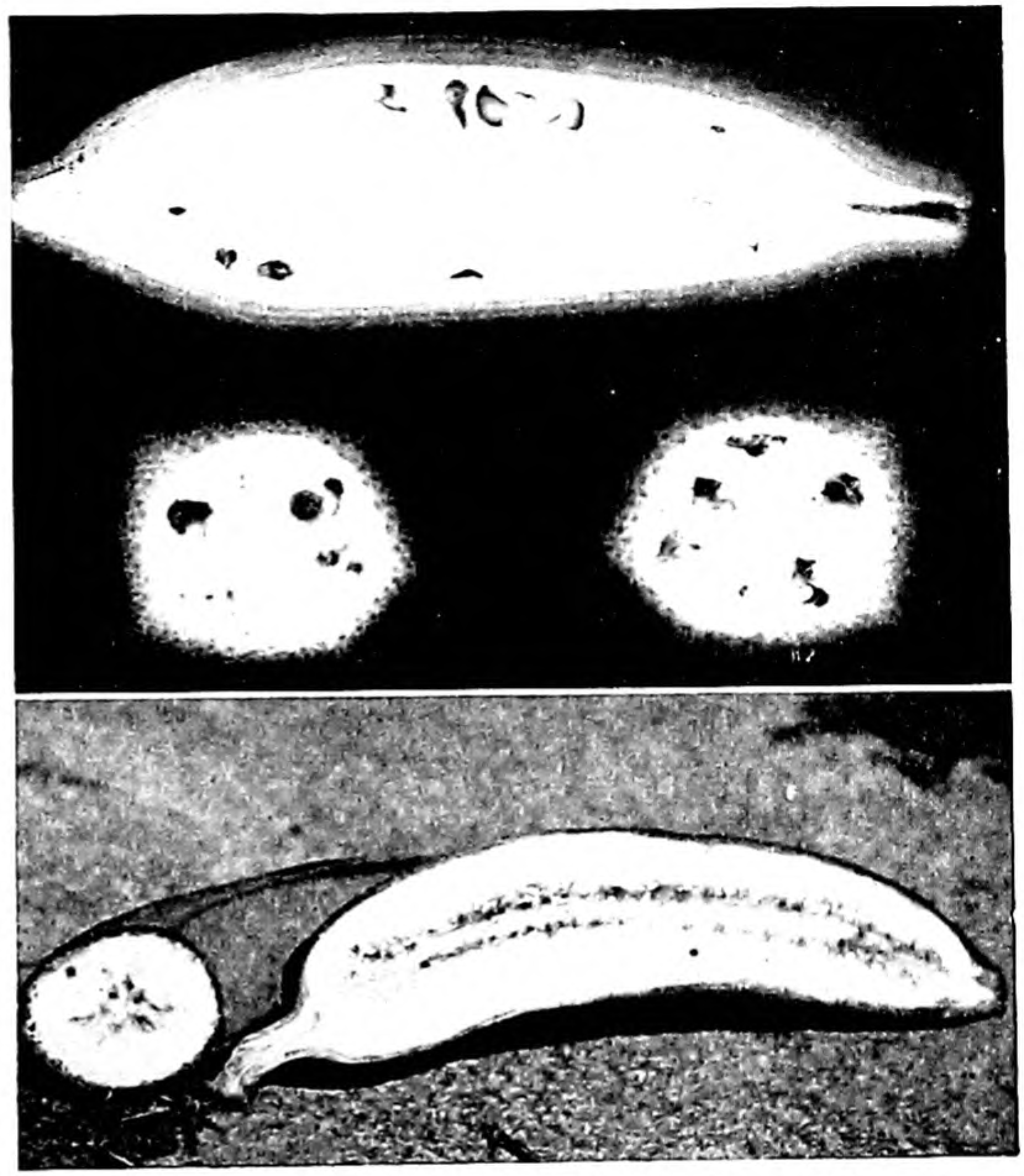


Embryos. (*Right*) *Zannichellia*, a primitive monocotyledon. (Redrawn from Coulter and Chamberlain, after Campbell.) (*Left*) *Capsella* at about the same stage of development.

similar to those of beans (see p. 322). The mature peanut has no endosperm.

PARTHENOCARPY. In some plants in which fertilization cannot occur, or where perfect seeds do not form, the mere growth of the pollen tubes provides sufficient stimulus to cause full development of the ovary wall. Pollen is known to be a rich source of auxins which are probably important in causing the growth of fruits even when seeds are not formed. Well-known examples of seedless fruits are the ordinary banana, pineapple, and certain grapes, oranges, and grapefruits.

The development of a fruit in this way is known as *parthenocarpy*. By derivation, this word means "fruit production without fertilization." There are a number of possible causes of failure of fertilization in plants that exhibit parthenocarpy, but they often imply either an incompatibility between the egg and the sperm or poorly developed gametes. Parthenocarpous plants can be propagated by vegetative means only. Therefore, the various seedless fruiting types are perpetuated by the rooting of cuttings, by budding and grafting and, in the case of bananas and pineapples, by transplanting short stolons.



Banana fruits. (*Top*) Wild banana of the Philippine Islands showing numerous seeds. (Courtesy, Eduardo Quisumbing.) (*Bottom*) Parthenocarpous fruit of cultivated banana with only rudimentary seeds.

PARTHENOGENESIS. A considerable number of angiosperms produce seeds regularly without pollination. The common dandelion is the most familiar example. When applied to this kind of seed production, the term parthenogenesis implies "a beginning without fertilization."

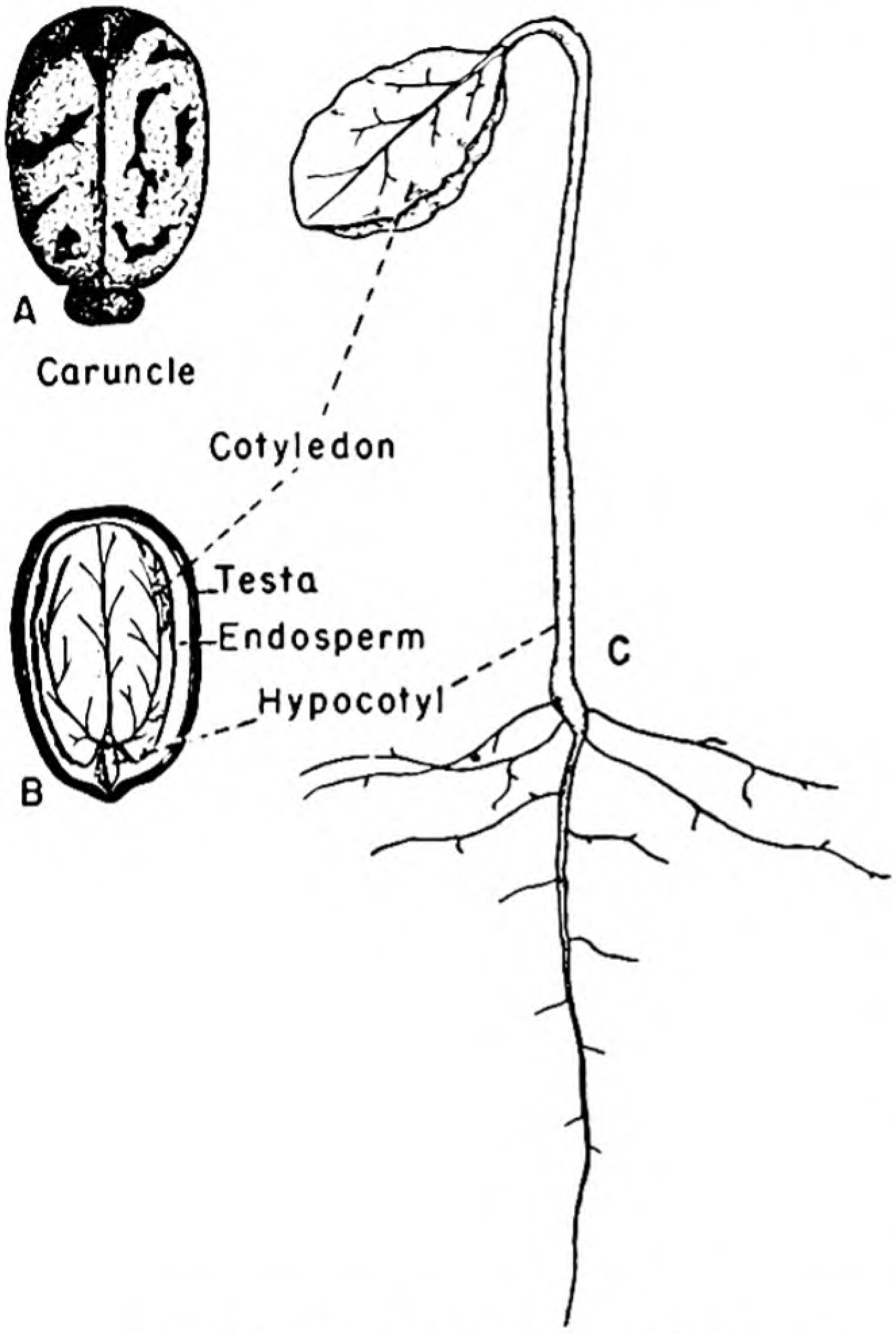
The underlying cause of this behavior is not known. The embryo sac apparently forms in the normal way except that reduction division does not occur. Hence the egg has the diploid number of chromosomes and develops directly into a normal sporophyte.

Seeds and Seedlings. Obviously the life history of an angiosperm is not complete with the formation of embryos. Instead, these embryos must resume growth, that is to say, the seeds must germinate, and the seedlings must become mature plants. Because there are several types of seed structure among angiosperms and because different seedlings do not behave alike, three representative kinds will be examined.

CASTOR BEAN. The seed of the castor bean plant, best known as the source of castor oil, consists of three separate parts: A hard *seed coat* or *testa* surrounds a soft, white oily mass of *endosperm* in which is imbedded the *embryo*.

The *embryo* is the most significant part of the seed. It is the young sporophyte, and the other parts are important only as accessories. It consists of a short axis bearing at its lower end the *embryonic*

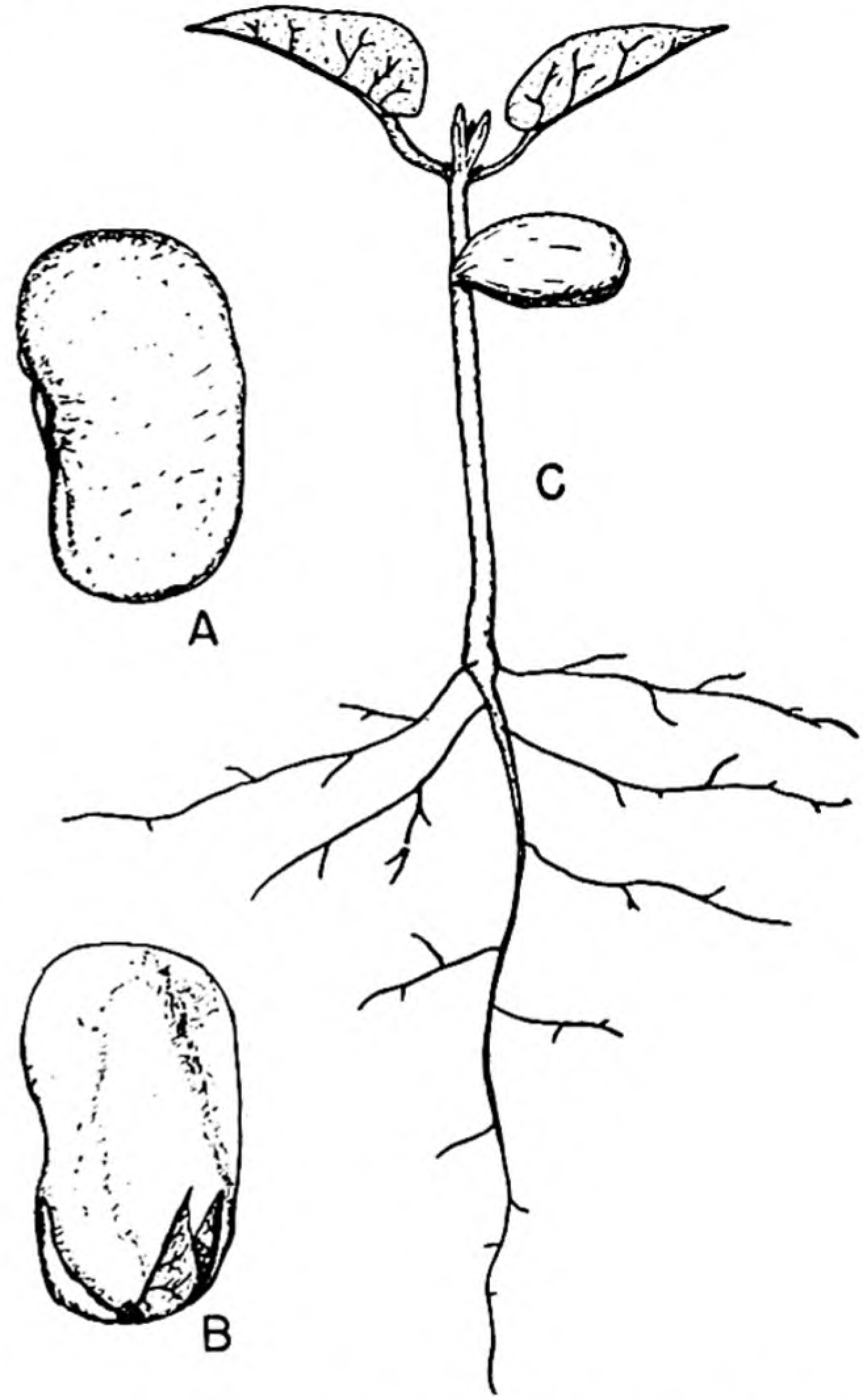
root which is essentially a meristem that acts as the forerunner of the primary root of the new plant. At the upper end of this axis is the growing tip, later to produce the shoot, and at its sides are two



Castor bean seed and seedling. (A) Castor bean seed, showing testa. At lower end is the *caruncle*, a spongy outgrowth from the testa. (B) Dissected seed showing leaflike cotyledon. (C) Seedling, showing development of cotyledons, hypocotyl, and roots. The epicotyl is beginning to organize the leafy shoot between cotyledons.

rudimentary leaves, the *cotyledons*. The point of attachment of the cotyledons marks a place where there is a rather definite change of structure and growth behavior. The portion below is commonly known as the *hypocotyl* (*hypo*, below), while the growing tip above is the *epicotyl* (*epi*, upon or above).

The *endosperm*, which may be defined as *food in a seed outside the embryo*, is rich in both oil and protein which are used as food by the young, growing plant when the seed germinates.



Bean seed and seedling. (A) Bean seed showing hilum, the oval scar at left center; micropyle, the small hole below hilum; and the general covering of seed, the testa. (B) Dissected seed showing one of the two large, fleshy, cotyledons; the two young leaves of developing shoot, the epicotyl; and (*at left*) hypocotyl, which narrows into the slender embryonic root. (C) Developing seedling showing (*from top to bottom*) epicotyl with two young leaves and growing tip; pair of cotyledons; hypocotyl; and developing root system.

The main function of the testa is to protect the other parts. The irregular coloration of the seed coat and the soft, spongy *caruncle* at one end,

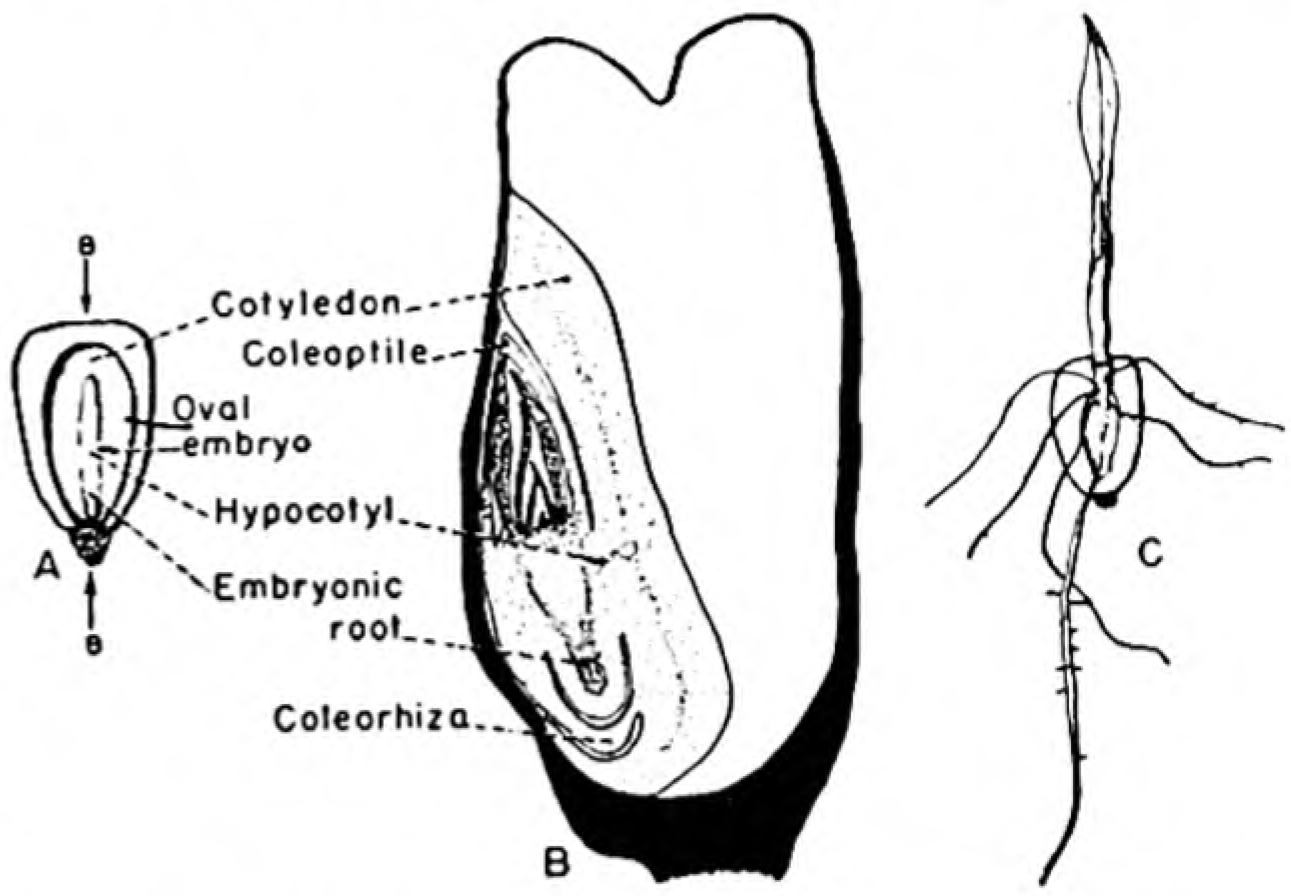
probably have no great significance, but the *hilum*, a small scar at the base of the caruncle, is the point at which the seed was attached to the placenta in the fruit. In other words, the hilum is the scar that appeared when the seed broke loose from the chalaza.

BEAN. An ordinary garden bean, as contrasted with a castor bean, is made up of only two parts—the embryo and the testa. There is no endosperm in the mature seed, the food that is used in the early growth of the seedling being stored in the cotyledons. The embryo is somewhat difficult to understand because its parts are peculiarly proportioned and arranged. The two large parts, with their flattened sides fitted together, are the cotyledons. They are so easily broken apart that they seem to be separate pieces, but both are attached to the summit of the hypocotyl. The hypocotyl is bent, causing the embryonic root and the terminal bud to point in almost the same direction. When the terminal bud or epicotyl is as large and well developed as this one is, it is sometimes known as a *plumule* (*pluma*, feather), because of the featherlike appearance of the young leaves.

The seed coat shows a distinct hilum at the middle of the concave edge of the seed. At one end of the hilum there is a minute opening, the *micropyle*, which is especially noticeable in a bean which has been soaked in water. The tip of the embryonic root lies near the micropyle.

CORN. A grain of corn is often mistakenly called a seed, but it is more than that, for its outer covering is actually the ovary wall. By definition, therefore, the grain is a fruit. The layers of tissue which would ordinarily have formed the testa have almost completely disappeared when the grain is mature, and the wall of the ovary serves as the protective covering and closely resembles a seed coat. This technical difference between the covering of a grain of corn and that of the other seeds under consideration should be recognized, but the two function in the same way. This type of coat is called the *pericarp* (*peri*, around; *karpos*, fruit) to distinguish it from the testa of a seed.

The elliptical or wedge-shaped depression in one of the flat faces of the grain marks the position of the embryo. Its parts and its relation to the other structures can best be seen in longitudinal section. There is a well-developed embryonic root enclosed in a special coat, the *coleorhiza;* an epicotyl surrounded by a *coleoptile;* and a hypocotyl, attached



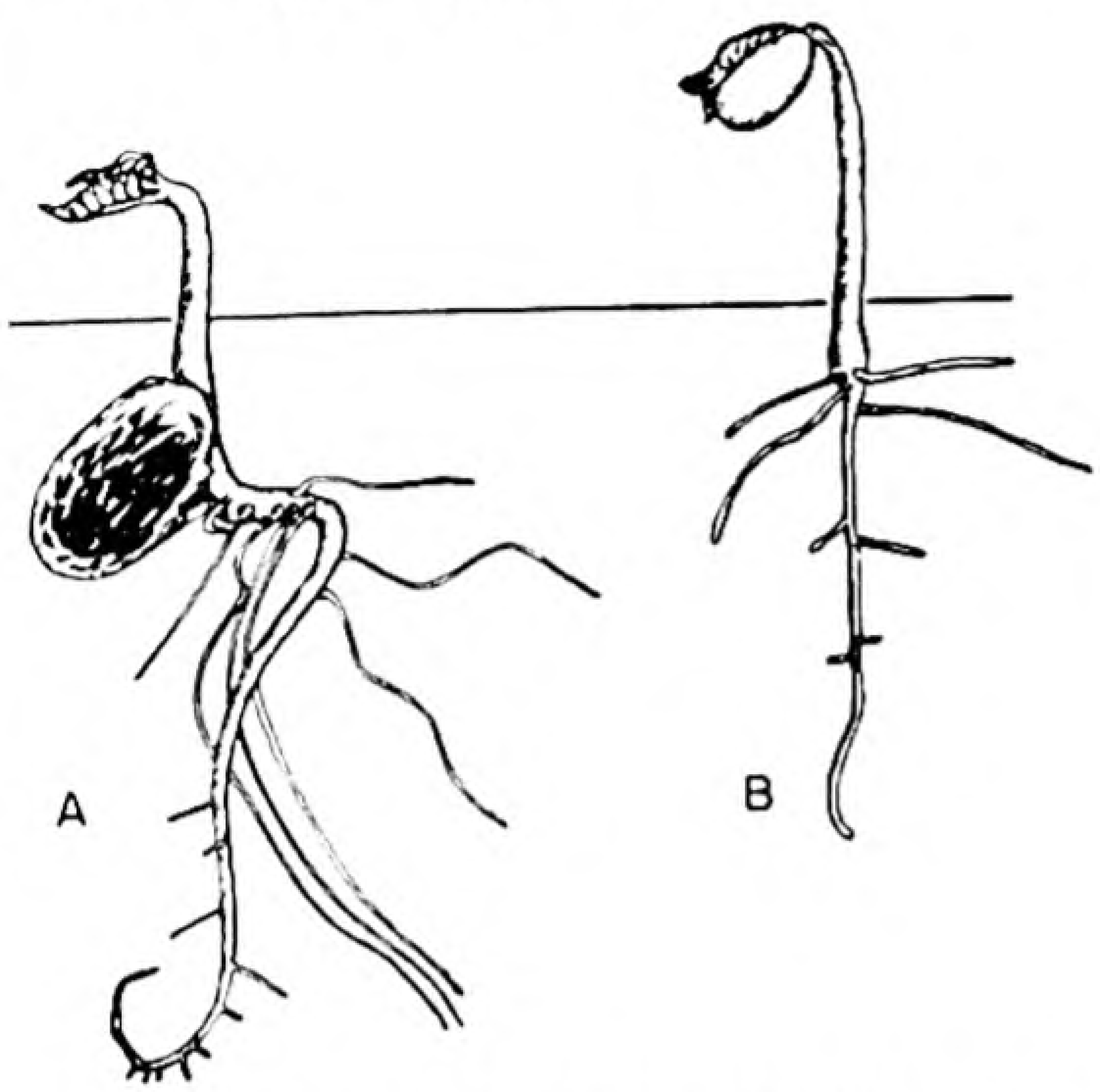
Corn. (A) Grain, showing position of oval embryo surrounded by a zone of endosperm. (B) Grain cut at right angle to flat surface. The outside covering is the pericarp, and the developing shoot above root and hypocotyl is the epicotyl. (C) Seedling, showing epicotyl developing into leafy shoot and roots growing out below. The hypocotyl does not elongate.

at one side of which is a *single cotyledon*. It is now possible to understand the original meaning of the name *monocotyledon*, for, as pointed out in the discussion of stem anatomy, the plant with a single cotyledon in its embryo almost always has scattered bundles in its stem and parallel veins in its leaves.

The greater portion of the grain is made up of the endosperm, which is probably more highly differentiated in corn than in any other plant.

GERMINATION OF SEEDS. Three conditions must ordinarily be present to bring about germination: there must be sufficient moisture, a proper temperature and, usually, oxygen. Seeds in storage may be warm enough and may have sufficient air to grow, but they lack moisture; those lying on the ground in winter have moisture and air, but temperature is too low; and those planted in a wet, compact soil or buried in mud may fail to germinate because they have insufficient oxygen. Some weed seeds are known to lie dormant deep in the soil for twenty or thirty years and then to grow freely when brought near the surface. The seeds of some aquatic

plants, on the contrary, are so well adapted to their environment that they not only germinate in the absence of oxygen but even fail if any appreciable amount of oxygen is present.



Types of germination. (A) Hypogeous germination of scarlet runner bean. (B) Epigeous germination of garden bean.

When a seed of the more usual type is suitably situated for germination, water is absorbed, oxygen enters, digestive and respiratory enzymes are produced, and the various growth processes are resumed. Either the hypocotyl or the embryonic root elongates, forcing the developing root tip through the testa. A positive geotropic response becomes evident in the young root, branches soon appear and all the tips become clothed with root hairs.

While these changes have been taking place, more or less enlargement has been in progress. If elongation is limited to the epicotyl, the cotyledons do not change their position but remain underground. This type is called *hypogeous germination*. If, on the other hand, the hypocotyl elongates appreciably, the cotyledons are lifted above the ground. This is *epigeous germination*.

During the early stages of germination it is necessary for the embryo to have both the building materials and the energy which are supplied by food. In seeds like the bean the food stored in the cotyledons is digested and transported to the points where growth is taking place. In those like corn and the castor bean, where the food is stored chiefly in the endosperm and is, therefore, outside the embryo, the cotyledons secrete enzymes that digest the endosperm and then absorb the food which the enzymes have made available.

As soon as the young plant has a root system well established in the soil and a stem and green leaves in the air, germination may be regarded as complete. This point is usually reached some time before the exhaustion of the food stored in the seed. When the seedling has reached maturity the life cycle is complete.

Inflorescences. The flowers of a plant may be solitary, that is, they may be produced singly on stalks arising from the axils of foliage leaves or from underground stems. On the other hand, they are often arranged in more or less complicated clusters. Any grouping of flowers on the plant is called an *inflorescence*. Since many important considerations hinge on an understanding of these arrangements, a brief examination of some of the more common types is necessary.

The main stalk of an inflorescence is known as the *peduncle*, and the stalk of each flower is a *pedicel*. Reduced or scalelike leaves associated with flowers or inflorescences are known as *bracts*. A whorl of bracts is an *involucre*. A *spathe* is a bract, or sometimes a structure composed of two or more united bracts, which encloses a flower or an inflorescence. A *scape* is a peduncle which rises from the ground and has no true foliage leaves, as occurs in most violets, the dandelion, and the lily-of-the-valley.

An analysis of all kinds of inflorescences shows two general types. In one of these the flowers are borne in the axils of leaves or bracts and, since the terminal bud is free to grow and enlarge the flower cluster indefinitely, this type is known as *indeterminate*. In a *determinate inflorescence*, on the other hand, the apical meristem of the peduncle organizes into the parts of a flower. Therefore, no additional buds can form at the tip of the floral axis. For this reason all the younger flowers of such an inflorescence develop from branches that form below the tip. In other words, a determinate inflorescence produces blossoms from the top downward or from the center outward, and an

Indeterminate inflorescence of evening primrose. Maturing seed pods are to be seen below the flowers and a series of younger and younger buds is forming above.

indeterminate one from the bottom upward or from the margins inward.

Determinate inflorescences are commonly called *cymes*. Good examples are seen in the chickweeds and in strawberry, raspberry, and blackberry. In these berries it will be remembered that the terminal fruit in each cluster is the first to ripen.

Indeterminate inflorescences are much more numerous than determinate, and a number of types are recognized by the differences in the arrangements of the flowers. Although the several types may have been evolved in various ways, it is convenient, for purposes of description, to regard them as modifications of one simple form, and the raceme to be described below can be used in this way.

A *raceme* is a simple indeterminate inflorescence in which the individual flowers are borne on pedicels attached directly to the main axis. Good examples are seen in larkspur, wild cherry, currant, sweet clover, and barberry.

A *spike* is like a raceme except that the flowers are sessile (*sedere*, to sit) on the main axis; that is, they have no pedicels but are attached directly to the main stalk. Good examples are the inflorescences of mullein, verbena, and some species of plantain.

A *corymb* is like a raceme except that it has a very short main axis and the outer pedicels are considerably elongated, in this way producing a convex or flat-topped cluster, as in red haw and some of the cherries.

Determinate inflorescence (cyme) of morning-glory.

Indeterminate inflorescences. (*Left to right*) Raceme of hollyhock, spikes of verbena, compound umbels of parsnip, and head of sunflower. In sunflower notice that the center flowers have not yet opened.

In an *umbel* the pedicels are all attached to the summit of the main axis. This type of inflorescence is characteristic of most species of the parsley family, such as parsnip, carrot, dill, and water hemlock; it is also found in many widely scattered species such as onion and milkweeds.

A *catkin* is a complicated, more or less tassellike scaly spike of such trees or shrubs as birch, poplar, hazelnut, hickory, willow, and oak. It is technically known as an *ament*.

A *head* is a rounded cluster of flowers which are attached directly to a short broad axis or receptacle. Some heads, such as those of clover, button bush, or sycamore, are simply compact aggregations of flowers of the ordinary types, but in the great composite family, flowers of a special form are crowded together on a flat or convex receptacle. The receptacle of such heads represents a greatly shortened axis, and the whorl of bracts making up the *involucre* often has much the appearance of a complicated calyx (see right-hand photograph above).

Besides these simple inflorescences there are innumerable compound and combined forms, made up of simple units. Some of these can be designated as compound corymbs or umbels, while compound racemes are called *panicles*.

Types of Pollination. As applied in the angiosperms the term *pollination* means the transfer of pollen from the anther in which it develops to a stigma. A considerable vocabulary has been built up to describe various types, based on the facts that pollen may become attached to a stigma in the same flower, that it may reach another flower on the same plant, or that it may be carried to some other plant.

A large number of terms to express these differences has relatively little value, for a knowledge of the behavior of chromosomes and the genes they carry leads to the supposition that the same results should be expected from pollination within the same flower as from that between two flowers on the same plant. Experiments support this theory. Therefore, the transfer of pollen from an anther to a stigma on the same plant, whether within the same flower or not, properly may be called *self-pollination*, while that between flowers on different plants is *cross-pollination*.

Most angiosperms have *perfect flowers*, that is, those in which both stamens and carpels are present. They are, therefore, close together. In a considerable number of species, self-pollination is entirely successful because the pollen germinates

readily and fertilization ensues, but this is by no means a universal occurrence.

In many species the stamens and carpels of a given flower become mature at different times. Therefore, the stigma is not receptive when the neighboring anthers are releasing pollen. In a few species (for example, buckwheat, rye, cabbage, red clover and some of the orchids), even if the anthers and stigmas ripen at the same time, own pollen fails to germinate. In a somewhat larger number of species the pollen tubes grow so slowly that they only occasionally reach the ovules and therefore seldom bring about fertilization. This type of behavior is well shown in corn. If pollen from a given plant is placed on stigmas (silks) of that same plant and all other pollen is prevented from reaching them, only a few grains of corn are likely to develop. If the stigmas are dusted with a mixture of own and foreign pollen, a well-filled ear may be expected, the reason being that the tubes produced by foreign pollen grow very much more rapidly than do those of own pollen. They are able, therefore, to reach the ovules and bring about fertilization.

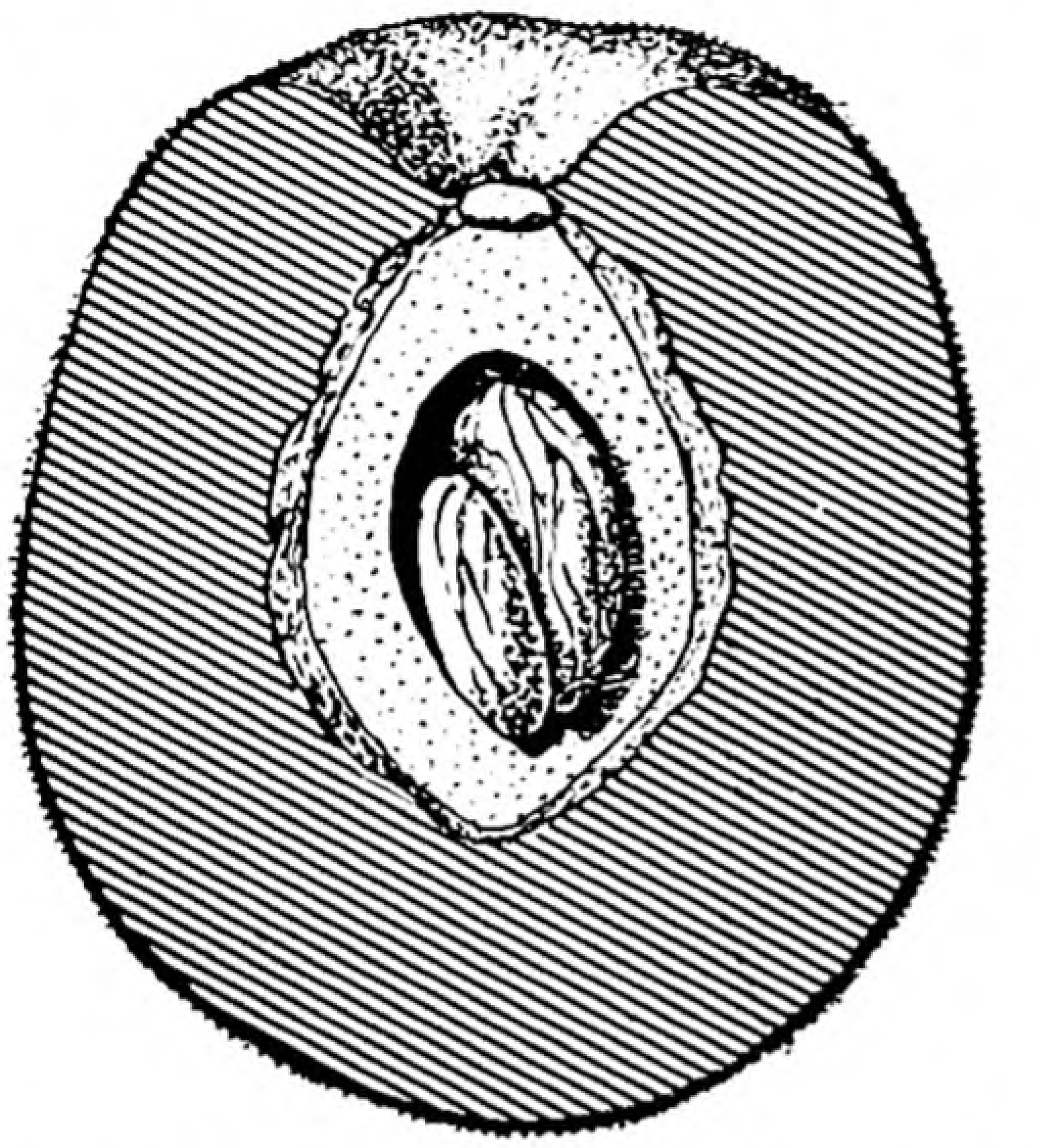
The cause for this type of behavior is understood only in part. It has been discovered, however, that in some self-sterile plants the placenta produces a secretion that diffuses through the style and inhibits the growth of the tubes of own pollen.

Pollination in yucca. (*Top*) A plant of *Yucca glauca* in flower. (*Bottom, left*) A few flowers near natural size. The open flower near the bottom shows the small white moth that acts as the pollinating agent, clinging to the top of the style. (*Bottom, right*) Seed capsules showing holes made by larvae of the insect in their escape to the ground.

SELF-POLLINATION. The idea is prevalent that self-pollinated plants cannot be successful. This is far from the truth. In many species, cross- and self-pollination seem to be equally effective, while

in others, as for instance, in the garden pea, cross-pollination seldom occurs except by accident.

An even more striking situation is found in *cleistogamous flowers*. These are flowers that never



Fruit of peach split in half showing the two seeds in the single cell of the ovary whose wall, the pericarp, has ripened as an inner stony endocarp and an outer fleshy, edible layer.

open. Instead, the pollen within the anthers is either shed directly onto the stigma or, in some cases, the pollen tubes grow more or less directly from the anthers to the ovules. While these flowers are seldom noticed they often produce remarkable numbers of vigorous seeds. Probably the best known plants with cleistogamous flowers are some of the violets. At the end of the spring season during which time the attractive open flowers appear, the violet plant frequently develops numerous flower buds under the surface of the soil. During the summer these buds organize pistils and stamens. Then fertilization takes place and seeds mature.

Numerous other plants, as *Oxalis* and some mints and grasses, have cleistogamous flowers, at least occasionally.

In some plants self-pollination takes place regularly through the activities of insects. For instance, bees flying from flower to flower on a fruit tree distribute pollen chiefly from that tree to the stigmas of its own flowers or occasionally they bring about cross-pollination by going to other neighboring trees of the same kind. Pollination in all such cases as this is incidental to the actions of the bees in gathering pollen and nectar for food.

In a few species of plants elaborate behavior patterns are carried out by the pollinating agents. As an example, the pollination of the various species of wild yuccas of the southwestern United States is brought about by small white moths of the genus *Pronuba*. Without these little moths there would be no yucca seed and without the yucca flowers the moths could not produce young, so closely are the lives of these two organisms intertwined.

When the flowers are open the female *Pronuba* forces her ovipositor through the wall of the ovary of the yucca flower and deposits eggs. Then she gathers a load of the rather sticky pollen grains and fastens them securely to the stigma. As a result, pollen tubes form, fertilization takes place and the ovules become seeds.

While these changes are in progress the eggs of the moth hatch, producing the wormlike larval stage of the insect. This is the stage in which the young moth does little aside from eating and growing. It supplies itself with food by devouring the developing seeds. But the larva is not large, and keeping itself gorged until it is full-grown destroys only about 24 of the numerous yucca ovules.

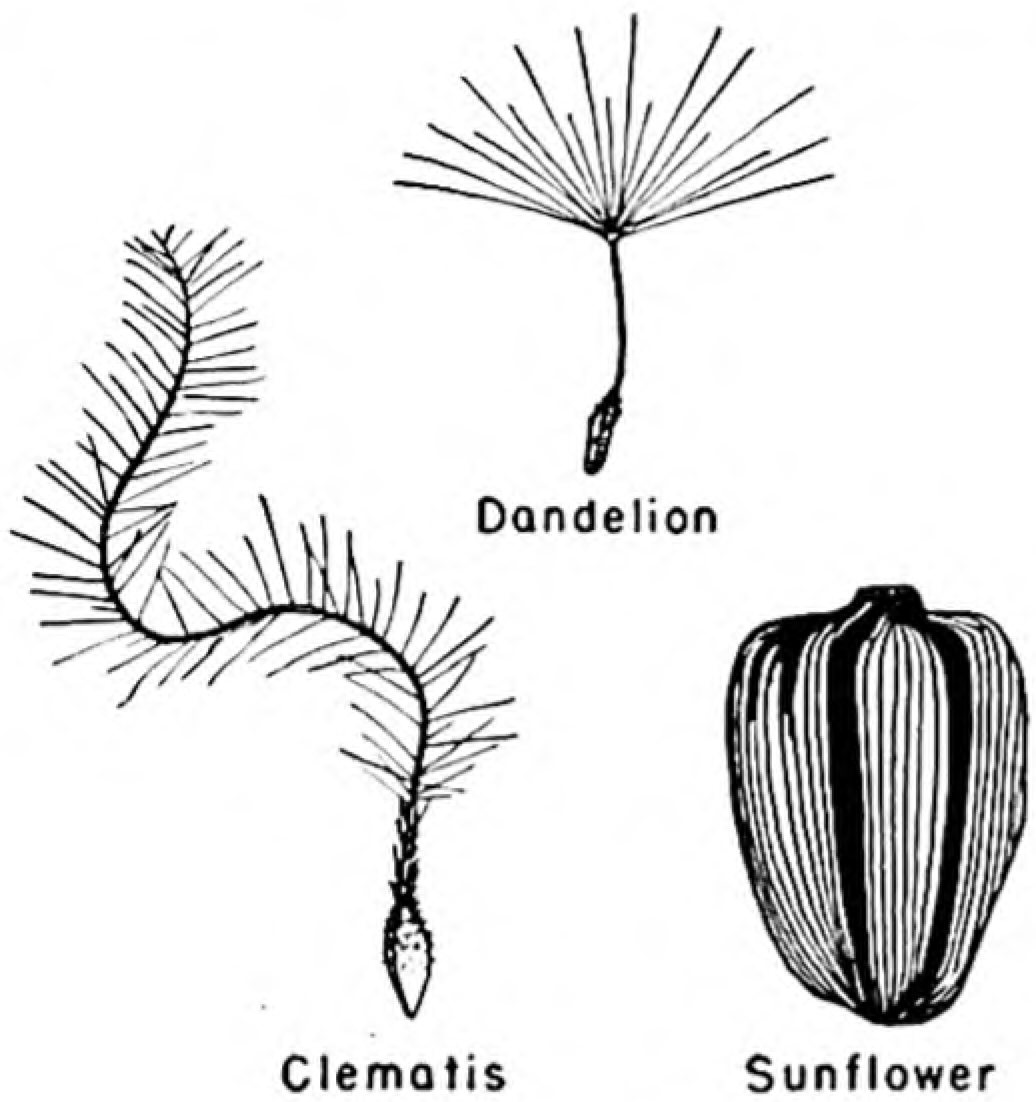
In the autumn each full-grown larva cuts a hole through the ovary wall and falls to the ground where it burrows in and goes into the quiescent pupa stage.

By spring the wings and other adult structures have organized and at the time the yuccas are in flower the adult moths emerge and mate. Then the females go through the routine of depositing eggs and planting pollen as their mothers did a year before.

CROSS-POLLINATION. The example just given is one of many in which insects are instrumental in bringing about self-pollination. They also carry pollen from plant to plant, often in a systematic way. The other agency that is very effective in bringing about cross-pollination is the *wind*.

Wind-pollinated plants usually produce large

amounts of light, dry pollen and have widely spread bushy stigmas in which the grains become ensnared. Even a light breeze may carry numerous pollen grains, many of which become attached to



Achenes.

the stigmas. That this is a successful method is attested by the fact that such plants as the grasses, cottonwoods, oaks, and birches are definitely wind-pollinated.

Types of Fruits. Following the flower comes the fruit. In the broadest sense, *a fruit is any structure which develops from a flower or inflorescence after the time of pollination.* In a more limited sense, *the fruit is the matured ovary containing one or more seeds.* When the ovary is inferior, that is, embedded in the receptacle, the surrounding tissues ripen with the ovary wall and become a part of the fruit, as in the currant or pumpkin.

The wall of the fruit is called the *pericarp* (*peri*, around; *karpos*, fruit). In such fruits as the peach or cherry, the pericarp ripens in the form of two layers, the outer one being fleshy and the inner one stony. Therefore, what is usually called the "seed" of one of these fruits is actually one or two seeds surrounded by the stony *endocarp* or, in other words, the inner layer of the pericarp.

A fruit that is made up of many distinct carpels is *aggregate* when, as in the blackberry, the whole structure is produced by a single flower; or *multiple* when derived from many flowers as in the mulberry or pineapple.

There are so many kinds of fruits that a detailed treatment is long and complicated. Nevertheless, the following outline will enable the student to identify and classify the principal types.

FLESHY FRUITS. These are fruits in which all or a part of the pericarp is soft and juicy.

Berry. A berry is a fruit which is soft and pulpy throughout. Examples are grape, blueberry, gooseberry, cranberry, tomato, and currant.

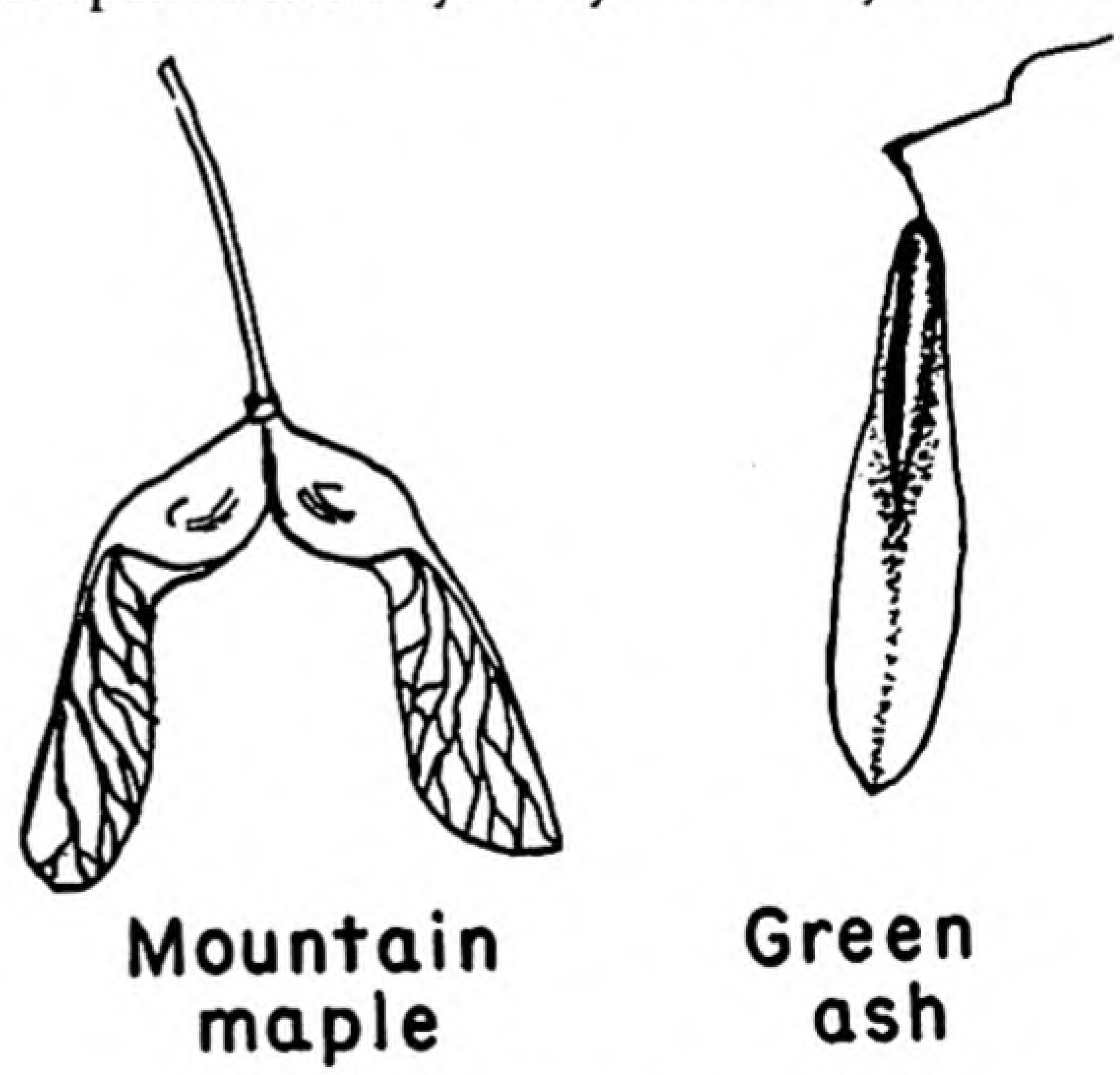
Pepo. This is the characteristic fruit of the gourd family. Well-known examples are pumpkin, cucumber, and melon.

Pome. This is a fruit with a core. The best known representatives of this type are apple, pear, and quince.

Drupe. This is a stone fruit, that is, one in which the endocarp is hard and stony. This type includes such fruits as peaches, cherries, plums, and the individual parts, or drupelets of blackberries and raspberries.

DRY FRUITS. In these fruits the pericarp is dry at maturity.

INDEHISCENT FRUITS. These are fruits that do not split open at maturity. They are usually one-seeded.



Samaras.

Achene. This is a small fruit that is often mistaken for a seed. The outside covering is the ovary wall to which the testa of the single seed is partly adherent. The pericarp often bears a feathery

appendage derived from the style, as in clematis, or it may have teeth or hairs representing a modified calyx, as in Spanish needle, dandelion, or thistle.

Caryopsis. This fruit is similar to an achene, but with the seed coat lacking or inseparable from the pericarp. It is the characteristic fruit of the grasses, including corn and wheat.

Legumes.

Nut. A nut is like a large achene with a hard, bony wall, often with a covering husk. Examples are acorn, chestnut, hazelnut, coconut, and walnut.

Samara. This is an achenelike fruit with a wing. Examples are ash, elm, and maple.

DEHISCENT FRUITS. These are fruits that open in some characteristic way at maturity. They are usually many-seeded.

Follicle. This is a fruit which splits along one side. Examples are the fruits of peony, larkspur, and milkweed.

Legume. This is a fruit that splits along two sides, forming two *valves.* It is a peculiar kind of pod that is characteristic of the pea family. Examples are bean, pea, and peanut.

Loment. The loment is a legumelike fruit constricted between the seeds and breaking crosswise. The best-known example is the beggar tick.

Capsule. A capsule is a fruit developed from a compound pistil and splitting in some definite way as in the jimson weed, morning-glory, evening primrose, lily, iris, and pink.

Classification of the Angiosperms. Here, as elsewhere in the plant kingdom, the ideal should be to discover kinships as bases for the various steps in classification. First of all, the subdivision, Angiospermae, falls naturally into the two classes, *Dicotyledonae* and *Monocotyledonae.* The dicotyledons, as the name implies, have two cotyledons in each seed and a monocotyledon seed has one. Careful comparison makes it obvious, however, that the difference between these classes is far wider than a mere divergence in seed structure. Attention has already been called to the fact that the type of stele and the arrangement of veins in the leaves are quite distinct in these two. Floral characteristics likewise clearly separate them. On the other hand, many features show that there is a definite though distant relationship between them. The present tendency among botanists is to consider the monocotyledons to be highly specialized derivatives of the dicotyledons.

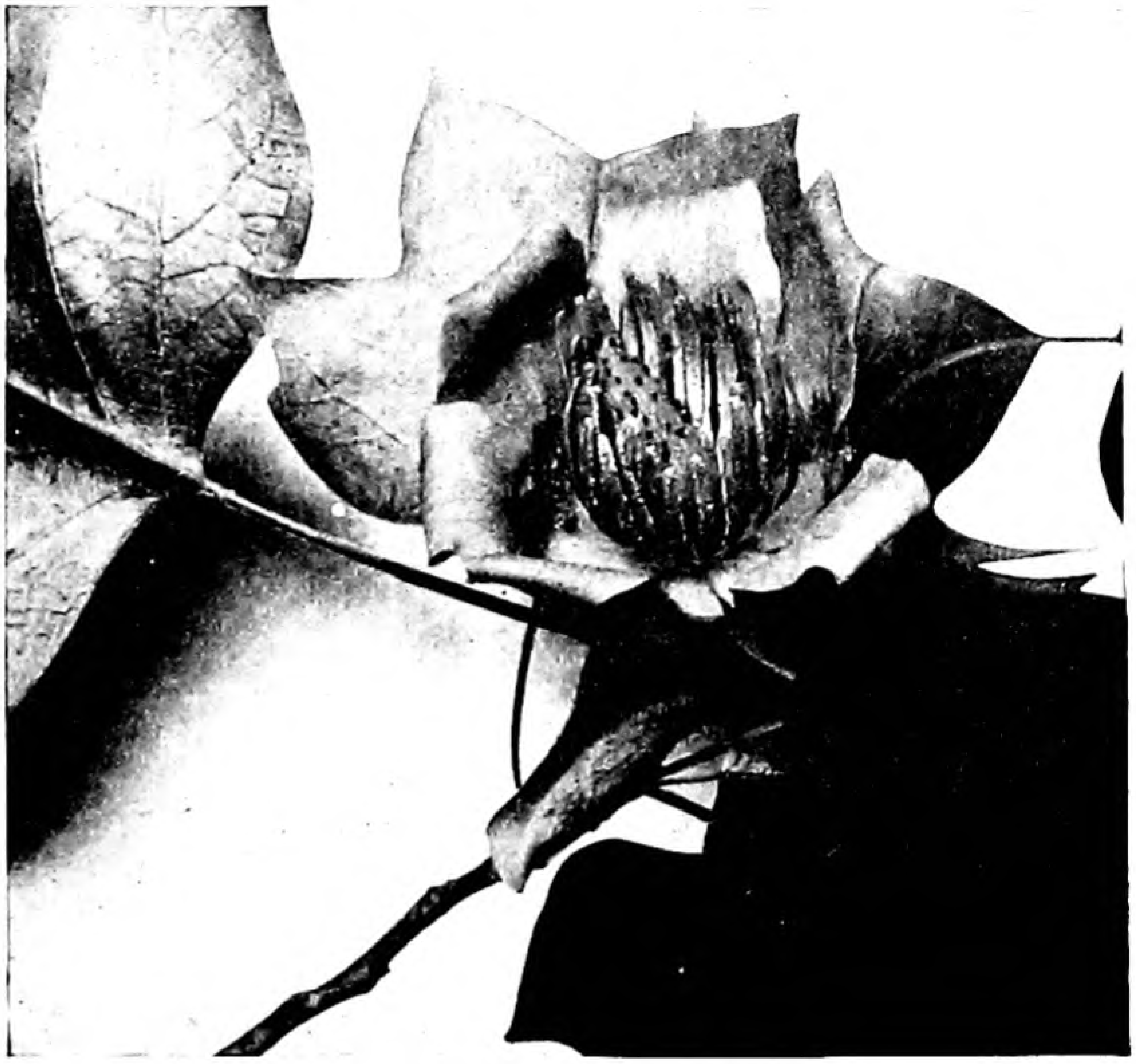
Capsules of evening primrose.

THE DICOTYLEDONS. This branch of the angiosperms is very much diversified into numerous large orders. There is a considerable amount of disagreement among botanists as to the most primitive of these and at this point known geologic

history gives almost no help. For this reason it is impossible to outline relationships with as great a degree of certainty as one would wish. Much investigation is being carried on and it is to be hoped that within the next few years great progress will be made in knowledge of the actual kinship among the angiosperms.

This great class, the Dicotyledonae, is so large and complex that there would be little value here in giving detailed descriptions of all the orders and families that are included in it. Instead, a few of the more prominent ones will be described briefly.

There are some indications that evolutionary changes have taken place along three rather diverse lines since primitive angiosperms first appeared. The reason for such a concept is based almost entirely on comparative floral structure, for the fossil record gives only indefinite hints as to the origin of the various groups.



Flower and leaves of tulip tree.

The following abbreviated outline is built around the hypothesis that the present-day order most like the ancient ancestral angiosperms is the one called the Ranales, and that out of such a group there have developed the monocotyledons and two rather distinct lines of dicotyledons.

RANALES—BUTTERCUP ORDER: *Magnoliaceae—Magnolia Family.* The members of this family are woody plants, chiefly of tree size. The best known are the magnolias and the tulip trees. The flowers have large sepals and petals. Stamens and carpels are numerous. Each individual part of the flower is attached directly to the cone-shaped receptacle.

Ranunculaceae—Buttercup Family. These are the buttercups and their relatives. The flowers follow almost the same general pattern as those of the magnolias, but with considerable variation. This is a family of herbs with the slight exception of a few species of small woody plants.

Besides the buttercups this large family includes the columbines, larkspurs, marsh marigolds, anemones, monkshoods, peonies and clematis, to mention only a few that are rather well known.

Other families of the Ranales include nutmeg, sassafras, camphor, cinnamon, avocado, May apples, barberry, and water lilies.

MALVALES—MALLOW ORDER: *Malvaceae—Mallow Family.* The most important of all the members of this family, from the human standpoint, is cotton, and probably the most widely known is hollyhock. A considerable number of weedy plants, ornamental herbs, and shrubs also belong to this group.

Floral characters sharply set these plants off from all others. As in the buttercups, sepals and petals are present and there are numerous stamens and carpels. In contrast with the Ranunculaceae, however, the stamens tend to be united at the base into a tube around the carpels and also to be attached to the base of the corolla in such a way that they and the corolla fall away together in one piece after the pollen is shed.

(*Top*) Columbine. (*Bottom*) Water buttercup.

Many botanists believe that this family is one of several that have specialized, each in its own way, from the buttercup family.

PAPAVERALES—POPPY ORDER: *Papaveraceae—Poppy Family.* The floral characters of poppies are only slightly altered from those of the buttercups. The greatest divergence from that family is that the carpels instead of remaining distinct from each other, are organized into a compound pistil that ripens in the form of a capsule.

Cruciferae—Mustard Family. This large family includes such cultivated plants as cabbage, radish, and turnip, as well as some of the most widespread and persistent weedy mustards. The pattern of flower is reduced to four sepals, four petals, six stamens, and two carpels which, together, form the compound pistil.

POLEMONIALES—PHLOX ORDER. This order contains many well-known members such as the phloxes, morning-glories, heliotropes, forget-me-nots and nightshades. The definite set of characteristics they share clearly indicates their relationship to one another. All have five sepals, five petals united into a single tubelike corolla, five stamens attached by their filaments to the wall of the corolla tube, and usually two or three carpels forming a compound pistil.

Polemoniaceae—Phlox Family. These are the phloxes or sweet Williams of the woods, grasslands and flower garden, together with a considerable number of gilias of the western United States. The majority of these species are sufficiently showy and ornamental to attract attention.

Solanaceae—Nightshade Family. The nightshades are well known for several reasons. Some of them are important cultivated plants. Among these are potatoes, tomatoes, eggplants, tobacco, red peppers, and petunias. Others, as the buffalo bur of the West and Jimson weed throughout the country, have

Hollyhock. Note numerous stamens forming a column by their united bases.

powerful prickles on their capsular fruits, making these plants great nuisances. And finally, numerous members of this family are distinctly poisonous. Some are poisonous weeds that are fortunately only seldom eaten by livestock because they are distasteful. Even potato tubers that have been exposed to the light and have turned green sometimes cause death to persons who eat them.

LAMIALES—MINT ORDER: *Labiatae—Mint Family.* Most people know the mints because of their rich spicy odors. A few members of this family that are easily recognized are peppermint, spearmint, lavender, rosemary, catnip, horehound, sage, pennyroyal, and thyme.

The flowers are peculiar in having a tube-shaped corolla that takes the form of two lips. Each flower commonly has either two or four stamens attached to the inside of the corolla tube. The two carpels usually ripen in the form of four small hard nutlets. The stems of these plants are square and have opposite leaves though in a few species the leaves form whorls.

The verbena family is closely related to the mints and is included in the same order.

ROSALES—ROSE ORDER. This order is placed at the beginning of what is considered to be the second great evolutionary series arising from ancient Ranales.

Rosaceae—Rose Family. Besides the roses, both wild and cultivated, this family includes a vast assemblage of other common plants among which are the apples, pears, hawthorns, strawberries, raspberries, blackberries, peaches, plums, cherries, and bridal wreaths.

The members of this family are very much like the buttercups in many respects. The numbers of floral parts are similar in the two families, but in the Rosaceae the receptacle, instead of taking the form of a cone, is usually somewhat cup-shaped with the carpels either standing up or embedded in the bottom of the cup.

Leguminosae—Pea Family. This is one of the really remarkable families of plants. It includes peas, beans, peanuts, the various clovers, alfalfa, locust trees, redbuds, lupines, loco weeds, mesquite, palo verde, and hundreds of others that are common over larger or smaller areas. Some of these are important foods for man and his animals; some are highly prized decorative plants; others produce powerful drugs used in medicine; while still others cause severe losses to stock raisers because of the dangerous poisons they contain.

The flower is a rather well standardized structure. While there is some diversity, the usual form has five sepals, five petals, ten stamens and one carpel. The outstanding peculiarities of these flowers relate to the petals and stamens. The petals are so arranged as to produce the flower characteristic of the pea. Relatively, the upper one is very large, often entirely enclosing the remaining four before the bud opens. This large petal is called the

Morning-glory flowers.

Flower of false raspberry.

standard. Just below the standard are two others, one on either side of the flower. These are the *wings.* Finally, at the lower part there are two small petals that are somewhat united at their edges, often forming a structure called the *keel* which it resembles. More or less confined within the keel are the carpel and 10 stamens. These stamens are commonly in two groups: nine that are more or less united into a unit, and one standing somewhat apart from the rest.

ASTERALES—ASTER ORDER: *Compositae—Composite Family.* This is an enormous family of which the following representatives will serve as illustrations: dandelion, lettuce, dahlia, thistle, cosmos, sunflower, goldenrod, aster, chrysanthemum, and burdock.

In these plants the structure that is commonly called the flower is, in reality, a group of small ones crowded into a head and surrounded by an involucre like a calyx. Each individual flower consists of the usual parts arranged in a peculiar way. At the base is the ovary containing a single seed; sepals that may take the form of teeth, chaffy structures, or hairlike outgrowths called pappus grow from the top of the ovary; in addition, there are five stamens, the anthers of which adhere, forming a tube around the style and stigma. The corolla, also attached to the top of the ovary, is sometimes tubular throughout its length and sometimes the upper part extends outward in the form of a strap. The fruit matures as an achene.

Leguminosae. (*Left*) False indigo. (*Right*) Wild sweet pea.

THE MONOCOTYLEDONS. Earlier discussions have shown that the various dicotyledons usually have netted veins in the leaves and a basic stem pattern. This pattern shows a central pith surrounded by a more or less definite series of concentric layers, the innermost of which is xylem, followed in turn by cambium, phloem, cortex, and epidermis. The descriptions of the flowers have also shown that the sepals, petals, and stamens in each individual flower tend strongly to occur in fours, fives, and multiples of those numbers.

By contrast, the monocotyledon leaves have parallel veins and the stem almost never has a definite cortex or central pith. Instead, the vascular elements are usually in the form of small bundles irregularly distributed through a pithlike background. The floral characteristics also contrast sharply with those of the dicotyledons, for in the monocotyledon flower the prevailing number of parts is three.

Members of Lily Order. (*Left*) Mariposa lily. (*Right*) Wild iris. These represent the lily family and the iris family, respectively.

There are many botanists who are convinced that the monocotyledons originated from some ancient branch of the early Ranales. There is no known fossil record on which to base this theory, but there are two anatomic or morphologic reasons for the assumption.

The first of these relates to the cotyledons and the second to stem anatomy. Studies of the embryos of large numbers of angiosperms have shown that some of the Ranales have one cotyledon considerably smaller than the other, and in a few species, only one is well developed. Likewise, in some of the most primitive of the monocotyledons there is a small but definite vestigial cotyledon in addition to the large one. These structures are especially clear in the young, growing embryo before the seed has matured.

The stem anatomy does not especially suggest the Ranales, but rather dicotyledons in general. Although the monocotyledon stem characteristically has the scattered stele, the young seedling very often has a siphonostele, which soon becomes much dissected and then disarranged in the typical monocotyledon pattern.

LILIALES—LILY ORDER. This order includes several well-known families such as the iris, amaryllis and lily.

Liliaceae—Lily Family. There are large numbers of native and cultivated members of this family, some of which, as for instance the onions, are not commonly recognized as belonging here. On the other hand, the water lilies not only do not belong to this group, but are dicotyledons and members of the Ranales. The name, "lily," is so firmly attached to them that it is unnecessary to try to use some other term, but the botanist should recognize the fact that they have none of the characteristics that distinguish the true lilies.

A few of the members of the Liliaceae are tulip, mariposa lily, lily-of-the-valley, hyacinth, asparagus, tiger lily, Solomon's seal, trillium, yucca, crocus, and onion.

The characteristic flower has three sepals, three

petals, six stamens, and a pistil composed of three carpels. Sometimes the sepals and petals are almost alike and, in a few species, as in the Easter lily, they are adherent to each other in such a way as to produce a perianth tube.

Juncaceae—Rush Family. These plants resemble the grasses in appearance and are seldom noticed except by the botanist. They are included here because their flowers are practically like those of lilies, except that the calyx and corolla are chafflike structures.

GRAMINALES—GRASS ORDER: *Gramineae—Grass Family.* Whether one lives on the great grassy plains, in the tropics, in forested regions, or in deserts, he is familiar with some of the grasses. Bluegrass and Bermuda grass are common on lawns across the country; timothy produces great quantities of hay; and corn and sorghum are important crops as are also wheat, oats, rye, and barley. Even fishing poles are made from giant grasses, the bamboos. In addition to these that are generally known, there are hundreds of native species that are recognized only by specialists.

Origin of the Angiosperms. The fossil record of ancient angiosperms is very poor. Doubtless there are large numbers of deposits yet to be discovered, some of which may help to fill the gaps in our knowledge. The oldest undoubted angiosperm remains that have yet been discovered came from the lower Cretaceous period. They are estimated to be about 120 million years old. Others that are suspected of being related to this group belong to the Jurassic strata (see the table on p. 169).

Because of the uncertain and disconnected nature of these early records of floral structures it is impossible to have a clear idea of their form. In fact, the ancient angiosperms probably differed little from the flowerless ancestors immediately preceding them. This much can be said with certainty, however: the earliest known flowers were relatively simple, with small carpels, simple stamens, and flat or cup-shaped receptacles. These facts would lead logically to the assumption that the ancient angiosperms may have been derived from either some primitive gymnosperm line or even directly from an unknown scion of the Psilopsida.

Although the ancestry of the angiosperms is shrouded in obscurity, later developments are much more clear. By upper Cretaceous times there are known to have been considerable numbers of both monocotyledons and dicotyledons. Some hundreds of these can be assigned to modern families, although they do not represent species and genera that are living today. By the end of the Cretaceous period new forms seem to have been appearing with remarkable frequency.

Forests of pine, spruce, fir, hemlock, and Douglas fir still occupy large areas in the Northern Hemisphere, but it is equally true that these gymnosperms are gradually giving place to angiosperms that range in size from grasses to trees. Geologic history supports the statement that the angiosperms have been slowly but certainly replacing the gymnosperms during the last 100 million years, and there is every reason to believe that the process is still continuing.

SUPPLEMENTARY READINGS

Eames, "Morphology of Vascular Plants."
Haberlandt, "Physiological Plant Anatomy."
Johnson, "Taxonomy of Flowering Plants."
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Swingle, "A Textbook of Systematic Botany."

Chapter 22

PLANT COMMUNITIES; CONSTRUCTIVE FACTORS

"There is scarcely any biological task more attractive than that of determining the nature of the weapons by which plants oust each other from habitats."

—WARMING

Seeds and spores scatter all over the earth, and as many of them as chance to fall into conditions suitable for growth can be expected to produce mature plants. But so many plants sometimes begin to grow in a given area that a great majority of them cannot have access to nutrient minerals, light, water, or other necessities. Under these conditions, only those whose heredity best adjusts them to life in these particular surroundings are likely to live and produce offspring.

Out of these stresses there arise organized groups of plants (and animals, as well) whose life processes so well supplement each other that together they all form a blind coöperative. This organization is called an *association*.

But the presence and growth activities of organisms bring changes in the environment and with these shifts come alterations in the associations. Such alterations are called *successions*.

The following outline of the chapter should make clear some of the important forces which are at work and the results of their actions:

- Plant Associations
  - Dominant Species
- Plant Successions or Seres
- Community-building Forces
  - Dissemination
  - Survival after Dispersal
- Some Associations in the United States
  - Sugar Maple-Beech Association
  - Oak-Hickory Association
  - Bald Cypress-Tupelo Association
  - Ponderosa Pine Association
  - Short-grass Association

Somewhat less than a century ago a polished marble slab was erected to mark a burial place in central Indiana. Today, the headstone is so etched by the growth of several species of lichens that it is difficult to read the inscription. The growth in diameter of these little patches of primitive plants has brought some of them into contact with one another and they have now formed a very small and simple plant community.

A *plant community* can be defined as *all the plants growing in a given habitat*. Such a habitat may be a very small area, as in the example just given, or it may cover thousands of square miles of territory within a given set of climatic conditions. The term

Marble slab encrusted with lichens: a primitive plant community.

is a very inclusive and elastic one. For this reason many kinds of communities are recognized and a large vocabulary has been built up to express fine distinctions between them. Of these various types, that of the *association* stands out as especially important.

PLANT ASSOCIATIONS

A plant *association* is a community in which one or more species, known as *dominants*, play important roles in changing or controlling the environment. Because of these controls certain other species that are well adjusted to the conditions produced by the dominants may become established as a part of the association, while others, not so adapted, are excluded by their inability to live in this environment.

Dominant Species. Of primary importance in a plant association, as indicated in the last paragraph, is the group of dominants. The person who is beginning to gain experience in analyzing associations is usually somewhat at a loss to distinguish them. Probably the most satisfactory method is the observation of the effects of removal, one by one, of the various species that compose the community. The ones whose destruction brings about the greatest changes in the composition of the association are the dominants. Frequently, as in the example given below, it is possible to find places where such removals have already been made. Then the botanist has only to interpret the results which he sees.

It is obvious that the destruction of all the moss plants, all the ferns, all the violets, or all the lichens in a forest would cause only slight alteration in the community. In the Allegheny Mountains there are large areas covered with a forest composed largely of sugar maples, red maples, beech, white ash, two or three species of birch, perhaps a few white pines, and a considerable number of hemlock trees. Commercial interests in many places have carried on the experiment of destroying certain of these species over large areas, while leaving the others practically untouched.

Some fifty years ago the hemlocks in one such area were cut down and the bark removed to be used in the tanning industry. Rather earlier the white pines were taken because of their great value for lumber. To this extent, these losses changed the composition of the forest, but without destroying any of the primary characteristics of that community, such as the intense shade it cast or the rich humus in the upper layers of the soil.

More recently, the maples and beech trees came to be used as sources of wood alcohol and other distillation products. Their destruction produced a very different series of effects from that of the conifers. It was the beeches and maple trees that cast the dense shade and it was largely their roots that prevented the erosion of the soil. When these trees were cut down, the shade-requiring mosses, ferns, and almost all the herbaceous plants of the forest floor began to die; soil erosion set in; and within a few years an almost entirely new community of plants appeared. Soon, these mountain sides were clothed with an open stand of aspens

and with a ground cover of fireweeds, goldenrods, and other light-requiring species.

From these facts is becomes obvious that the controlling influence within the original forest was the sugar maples and the beech trees, for it was not until these were killed that any real revolution occurred in this forest. They were the dominants.

It is customary to name each plant association after its dominant species, or occasionally after the type of plant that exerts the controls. As examples, there are the maple-beech, the oak-hickory, the tall grass, the short grass, the piñon-juniper, the sagebrush, the creosote bush, the ponderosa pine, the longleaf pine, the bald cypress-tupelo, and the cattail-bulrush associations, to mention only a few that are easily recognized.

Biotic Associations. The habitable parts of the earth are populated, not with one or a few species, but with hundreds in almost any locality. Even a casual examination of any local association, however small, is likely to reveal representatives of several of the plant divisions as well as numerous animals. Interest in these studies has been focused on plants, but there is seldom a plant association that is not in reality a *biotic association* (*biotikos*, pertaining to life), as well. In other words, many kinds of organisms, including both plants and animals, live together, the various species affecting one another in more or less definite ways. One may choose any grove, grass plot, pond, or stream bank for study, and even though relatively few living organisms attract the attention at first, a thorough count of the species is sure to make an astonishing total, requiring a long time even to identify them all.

Every species of organism exerts its influence on every other one that lives in the same locality, for all reproduce at such a rate that only a very small percentage of the multitude of offspring can possibly have room in which to live or the necessary food to prevent starvation.

Green plants furnish food for all the rest, but when they become too crowded some of them die because they do not receive enough light to permit them to carry on photosynthesis. The molds and bacteria bring about the decay of all dead organisms, in this way nourishing themselves and at the same time returning nutrient minerals to the soil. Molds and bacteria are, in turn, held in check, first, by the limited amount of organic material available to them, second, by being devoured by such primitive animals as Protozoa, and finally by the antibiotic substances many of them are now known to produce. These, in turn, can live only as their food supply permits but they are the principal source of food for still other animals. Therefore, the fewer Protozoa there are, the less food they supply to their predators. This narrative might be continued almost indefinitely, for every one of these species either directly or indirectly affects every one of the others, and each tends in some way to restrict the numbers of all the rest.

A similar situation, but with variations, is to be found in forests, grasslands, or even deserts. In these associations various kinds of animals devour plants, or their parts, while others help to distribute pollen or seeds; and in a multitude of ways their activities are checks and balances on the entire community. Animals are so important in every well-organized association that the biotic community must be recognized as the real functional unit. The destruction of large numbers of the native animals of a region frequently affects the entire population of both plants and animals.

The beaver may be cited as an example. This animal is valuable in two ways. Beaver skins have long had a high commercial rating, even having been used as currency in Colonial days in this country. As a result, countless thousands of these animals were destroyed for their pelts, until there were only a few places in which they persisted in considerable numbers. Of late this grave error is beginning to be corrected, and they are being reëstablished in some of their old haunts.

The second value of beavers is less spectacular but far more important because of their mode of life. Long before man had learned to build check dams to prevent erosion, these animals had been building them for their homes. Beaver dams are constructed of logs, sticks, and mud, and are so placed that they form considerable ponds in which the animals live. They are usually built not far below the headwaters of streams, holding back large amounts of flood waters near their source

and allowing them to run out gradually. In this way the flow in such streams is regulated to a marked degree. After the beavers have been destroyed, the run-off following rain storms occurs quickly, making severe floods more likely in the lower parts of the rivers. With these floods comes disastrous erosion. Then, in contrast, water supplies run low at times when there is little precipitation.

The statement of these facts should make it clear that while the extermination of the beaver has added many thousands of dollars to the wealth of trappers it has caused losses of millions to society.

Small beaver dam in Rocky Mountains, showing impounded water. Note aspen stump in foreground where the animals got a part of their building material.

So great is the change in the plant and animal life within a stream and along its immediate banks, following the removal of the beaver that this animal very closely approaches the importance of a dominant. In no case, however, does any animal hold quite the key position in a community that is held by the dominant plant species. Even the beaver would not be able to survive without food and building materials provided by stream-side trees. The most important animals and the plants of secondary importance in a biotic community are often called *subdominants*.

The following discussion is limited to the vegetable part of the communities to be studied, except to call attention to some of the animal species that have pronounced effects on the entire functioning of these associations.

PLANT SUCCESSIONS OR SERES

Plants are able to migrate from one place to another, especially by means of seeds, spores, and rhizomes. But certain of the plant communities which they form, create changes in environment, allowing other associations to follow. The resulting sequence is called a *sere* or *succession*.

The first successful invaders of an uninhabited area are called the *pioneer species*. They are almost always capable of very rapid migration. Lichens, fireweed, aspen, and Russian thistle are good examples. In a new pond the pioneers are likely to be algae; on a bare rock, crustose lichens; and on freshly disturbed soils, various weedy plants. Climatic conditions, types of soil or other substratum (that is, water, rock, etc.) and the available species that can become invaders act together in determining the possible pioneers in any given locality.

When once established, the pioneers usually bring about changes in their physical environment that produce conditions suitable for other species. So nearly universal is this kind of activity that many examples could be given as illustrations. The principles involved will be shown in tracing the usual seral steps in a pond and on rock.

Pond Successions. The pioneer plants in a new pond are almost always some kinds of algae. Most of these probably gain entrance in the form of resting cells, zygotes, or occasionally as small vegetative fragments in the mud on the feet of water birds. With the algae, there often come seeds

or other propagules of hydric angiosperms, together with small animals or their eggs.

In a relatively short time a considerable collection of species of both submerged plants and swimming animals gains a foothold, the green plants synthesizing large amounts of food and aerating the water. Small animals eat algae and are, in turn, devoured by larger ones. In this way a food chain is established and a self-regulating community begins to be organized.

In very deep water the plants float and the animals either cling to them or swim. These plants are largely such algae as *Spirogyra*, *Zygnema*, and *Oedogonium*. With them are often associated the duckweeds, *Spirodela* and *Lemna*, or the little water ferns, *Salvinia* and *Azolla*. Living in this floating community or under its protection are large numbers of such floating, creeping and swimming animals as Protozoa, snails, insects of many kinds, and fish.

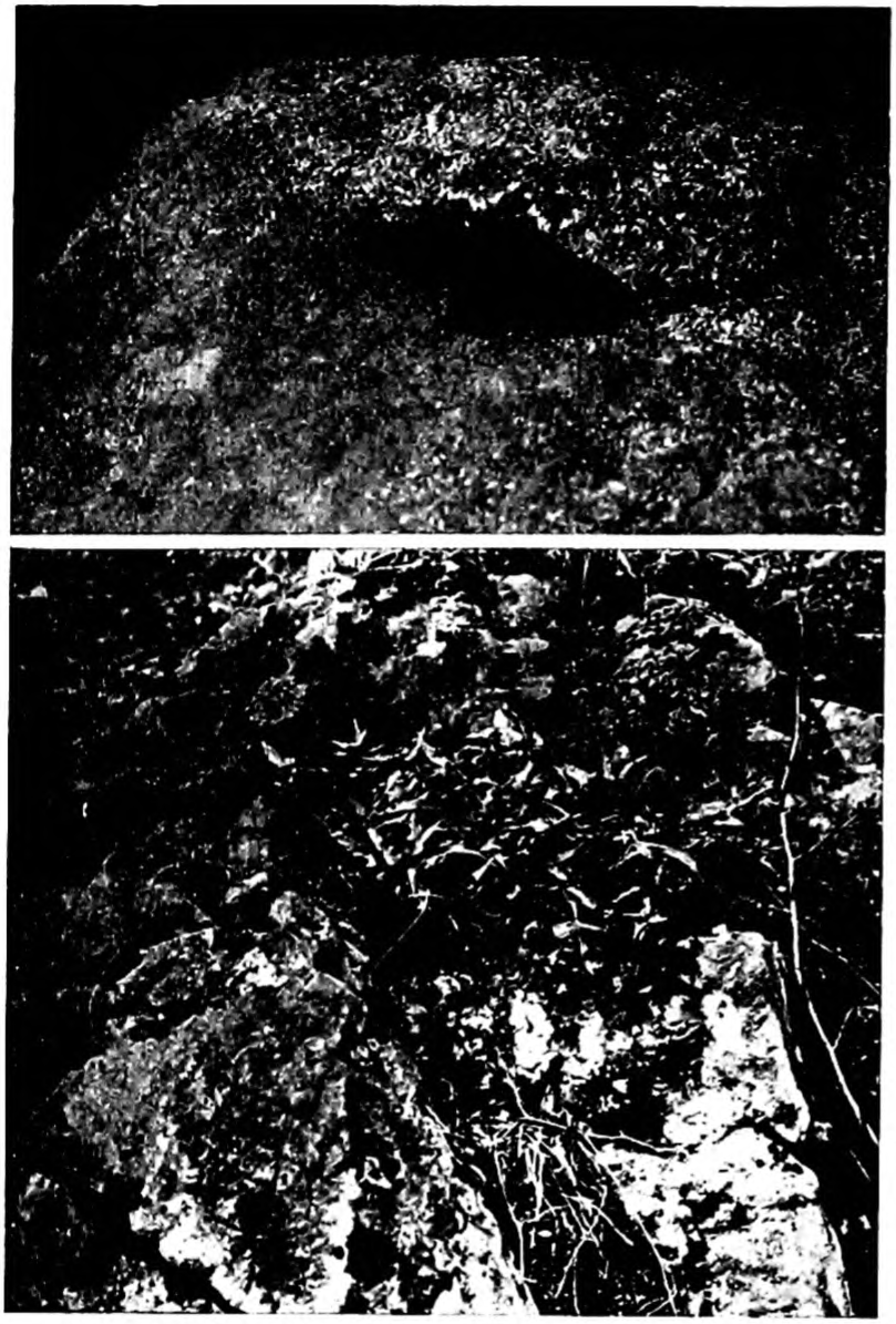
If the water is well supplied with dissolved calcium compounds, *Chara* is sometimes an important constituent of both the floating and later stages; or if the lake is contaminated with sewage, *Oscillatoria* may be common.

The excreta and dead bodies of the animals, together with decaying plant structures, and silt washed in from surrounding land, slowly but surely fill the pond or lake.

Whenever any part has become filled until it is only a few feet deep various kinds of rooted plants are likely to be established. Some of these are such submerged hydrophytes as pondweeds (*Potamogeton*), eelgrass (*Valisneria*), hornwort (*Ceratophyllum*), and *Elodea*. Others may be the various species of water lilies, whose leaves float on the surface, or even extend into the air. Under the shade cast by these plants, algae are almost entirely unable to grow because there is not sufficient light to permit them to synthesize enough food to maintain life. On the other hand, animals in large numbers congregate under the floating leaves.

In such communities humus is deposited rapidly, making the water shallower and producing conditions relatively unfavorable for the deep-rooted water lilies. Bulrushes (*Scirpus*), cattails (*Typha*), sedges (*Carex*), buttonbush (*Cephalanthus*), reed (*Phragmites*), and spike rushes (*Eleocharis*), are especially successful in the shallow water. They usually invade as rapidly as the reduced depth permits, crowding close to their vanishing forerunners. When once established, their vigorous

Pond in short-grass region showing zone of shrubby willows followed by grasses.



Rock successions. (*Top*) Crustose lichens with a few foliose forms over most of the rock surface, but in a small depression black moss has become established. (*Bottom*) A later step in succession in which larger amounts of moss are present; also foliose lichens, walking fern, and a few small seed plants.

roots and rhizomes elongate in every direction, occupying all the territory available to them.

On the muddy banks of a pond, a zone of shrubby willows, often interspersed with such herbaceous plants as water hemlock (*Cicuta*), iris, some of the mints, and smartweeds (*Polygonum*), usually appears. A little farther from the water there is commonly an additional zone of cottonwoods. Both the willows and cottonwoods come from seeds that are carried in by the wind.

If this pond is in the midst of a forest, these mud-inhabiting trees tend to merge with those of the higher, drier ground. In tropical and subtropical climates, the species taking part in the later stages of the sere are different from those named above, but the ecological effects are the same.

If, in contrast, the pond is surrounded by grasslands, the willow-cottonwood stage may be absent because the seeds are lacking. Whether these woody plants are present or not, the grasses characteristic of the region follow immediately.

As time goes on, the pond gradually fills, the margins become higher and less wet, and each zone encroaches on the one before it. Eventually the pond disappears and in its place there is dry land clothed with the vegetation of the region. This is the end of the sere.

Rock Successions. On a bare solid rock surface without any pockets of accumulated soil, there is seldom any pioneer that precedes some species of crustose lichen. These plants produce certain secretions that bring about slow dissolution of the rock. From this dissolved material they absorb the necessary nutrient minerals that are used in their metabolism.

Some of the cells of the lichen die, producing bits of humus which, when mixed with the particles of rock fragments, makes a slight trace of primitive soil. This soil may be held in place by the lichen or it may tend to accumulate in irregular depressions.

Even though amounts are small, this soil has more water-holding capacity and more available plant nutrients than the bare rock surface. These two improvements in the substratum permit soredia of some of the hardier foliose lichens to gain a foothold. When once established such foliose forms as *Parmelia* extend over their crustose

forerunners and cause their death by shading, in this way replacing them. The soil-forming capacity of the foliose forms can be demonstrated readily by removing the older, central part of an old thallus from a granite boulder. Underneath, there is likely to be a considerable layer of sandy clay from the disintegrated rock, and careful examination will sometimes show traces of humus from dying cells of the lichen.

From these and other sources considerable pockets of soil often accumulate in depressions in the rock surfaces. In these, the highly drought-resistant black moss, *Grimmia*, frequently becomes established. It forms a dense cushion, often almost an inch deep. The plant and soil, together, are very absorbent, holding moisture much longer than any of the lichens, and the humus produced by the decaying moss tissues, mixed with the clay-sand mixture, adds greatly to the available nutrients.

Seeds and spores of various plants, lodging in the moss cushions, germinate whenever there is sufficient moisture and when other conditions for growth are right. Some of the young plants that are of drought-resistant species continue to live, even when the water supply dries out. Then, with the next rain, growth is resumed.

The successful pioneer vascular plants are usually hardy grasses or such shrubs as sumacs, snowberry, or ninebark; or if the soil is distinctly acid, as it often is unless limestone is present, they may be blueberries or some of their near relatives. In dry climates they are likely to be some of the desert shrubs or more often very resistant ferns and species of *Selaginella*.

These rooted plants have two effects on the developing community. First their roots penetrate crevices in the rocks, widening them, slowly reducing the rock to fragments and second, most of them cast shade. This shade increases the relative humidity of the air, thus decreasing transpiration. It also makes conditions unsuitable for the light-requiring lichens, mosses, and grasses. In addition, the larger plants act as barriers to dead leaves, and to the run-off of water, still further increasing both moisture and humus accumulation.

Young trees springing up under the protection of the shrubs soon overtop them, casting so much shade that they are no longer successful. Thus, the sere ends, with the development of the forest.

Climax Associations. By some such series of steps, each sere ends, after a long period of time, in an established organization which does not give place to another. This final community is called a *climax association*. The type of climax which develops depends on climatic conditions. A sere on rock in the desert begins with crustose lichens just as one on rock in a humid climate does. Soil formation and accumulation may be slow in the extreme in the desert, but eventually seed plants adapted to arid conditions establish themselves and control the area. The species involved in the successions, from the pioneer lichens to light-requiring vascular plants, are not usually identical in the two habitats, but the steps of development are fundamentally the same. In a humid climate, however, the sere does not stop but goes on to a climax appropriate to that climate.

In a similar manner, all seres, wherever they occur on land, continue until they reach the climax determined by climatic conditions. A sere in a body of water in a desert eventually reaches a desert climax; in short-grass country, a short-grass climax; and in an extremely humid climate, such as that in much of the eastern United States, a maple-beech or oak-hickory forest. Likewise, a succession from a very dry habitat in any one of these localities reaches the same climax as does one from water in the same place.

Secondary Successions. If disturbances occur at any stage of a sere or in a climax, such as cutting or burning a forest, or destruction of the grass cover in the prairie, the succession is thrown back one or more steps, depending on the severity of the damage to the vegetation. If, for example, a fire sweeps through a forest, the trees are burned to charred snags; the decaying leaves and wood, as well as the humus, are largely changed to ashes; the nests of birds and squirrels are destroyed, and most of the adults of these animals are burned to death. Everywhere desolation reigns. Life is gone, with certain exceptions. Roots and rhizomes of some plants still persist; a few seeds and spores in the soil that were deep enough to be protected from

Secondary seres. (*Top*) Light-requiring aspens following forest fire. The next step is coming on in the form of young spruce trees growing in the shade of the aspens. (*Bottom*) Secondary succession following destruction of short grass by the great wagon trains of the Santa Fe Trail before the days of railroad transportation into the Southwest. The sere has almost returned to the original grass stage; few weeds now remaining. Near Dodge City, Kansas.

the heat remain alive; and some soil bacteria, some soil-inhabiting insects, and a few burrowing animals are safe.

Usually, light-requiring weeds and then aspens enter and become organized into an association that will persist over a period of several years. When these temporary dominants have begun to cast a considerable amount of shade, they make conditions suitable for the germination of the seeds of shade-requiring climax species. These seedlings may develop rapidly and when they are well established they are likely to overtop the light-requiring aspens, causing their death and reëstablishing the climax within a century or two after its destruction.

If, on the other hand, the fire is sufficiently destructive to burn most of the humus, the succession is likely to be carried back almost to the lichen stage. Under these conditions it may require not centuries but thousands of years to rebuild a balanced soil and reëstablish a forest similar to the original one.

Successions following interruptions of any kind are called *secondary seres*. One type that can often be seen in almost any locality results from such human activities as the building of roads, the making of railway cuts, or even the plowing of fields. In these and many other kinds of operations the original biotic community is entirely disrupted or even destroyed, leaving banks or level fields that are destitute of vegetation. In places like these, where the sere begins on disturbed soil, the pioneers are almost always some kinds of weeds. If the disturbance occurs in a woodland climate, shrubby species and young seedling trees are likely to appear in the shade of these weedy plants, but if it occurs in grassland there commonly follows a series of weedy communities. In either case, the secondary sere follows the same principles and most of the same steps as the primary succession.

A large scale destruction, a few years ago, of extensive tracts of the short-grass climax has proved to be a terrible mistake. Early in this century the American people destroyed much of the

sod of the great short-grass plains. The grazing of sheep and cattle in too great numbers weakened the grass and in many places the plow completed the killing.

Then, for a period of years, it transpired that there was little rain. The dry sandy soil, no longer fettered by the grass roots, was picked up by powerful winds and hurled skyward in gigantic clouds, only to settle in drifts in neighboring places. Crops were first uprooted and then covered by great piles of dust; domestic animals starved or died of thirst; and even the rabbits, field mice, and grasshoppers perished. Desolation seemed to be complete.

Then the weather cycle changed. Rains came; the drought was broken; seeds germinated, and plants grew to maturity. In some places certain fields had been abandoned during the worst years of the drought and here and there a few had no care for several seasons after the rains returned.

As if by magic these desolate areas became green almost as soon as the first summer moisture fell. It was not magic but the most usual of natural processes that clothed the barren soil with a thin coating of verdure. The very winds that had carried the dust of those storms had also hurled untold numbers of tumble weeds across the plains, scattering their achenes wherever they went; and with the grains of dust and sand these winds had sown myriads of small seeds of many other kinds. In this way the drifted soil became well supplied with propagules, ready to grow when the opportunity came.

If any of these areas should continue to be left to the processes of nature, a series of steps will be followed in the reëstablishment of the short-grass cover. The first of these steps in the sere will be made up primarily of coarse weeds that have little or no value except as soil binders. In the end, however, some 40 to 75 years from the date when the original grass was destroyed, the sere should return to the short-grass climax.

In the example given above, the seeds that germinated following the period of dust storms had been brought in from many directions. Some of them doubtless came from distant sources but the vast majority probably formed on plants that grew in small, isolated patches where they were somewhat protected, or in which the soil contained a little available moisture. These seeds became scattered from the centers of production almost as if they were following the laws of diffusion. That is, they traveled (were carried) from points of greater concentration (crowding) to more or less distant places.

If the original grass cover of the land had been left undisturbed, many of these weed seeds would have been carried in, but very few of them would have grown into mature plants. A well-established stand of grass exerts a powerful controlling influence that almost entirely excludes annual weeds, but when it is weakened or destroyed, the controls it exerts are relaxed and the weeds develop. In other words, the grass is dominant in the grassland climate.

COMMUNITY-BUILDING FORCES

It is almost impossible to keep any space in the habitable parts of the earth's surface free from organisms. A field is plowed or a lawn is graded and, unless much effort is put forth, the soil is soon covered with weeds; a pond is made and it becomes richly inhabited almost at once; and even the surgeon must take remarkable precautions to prevent the small surface of his instruments from becoming contaminated with living bacteria during the few minutes required to perform a simple operation. Everywhere, life seems to be ready to spring into action at the slightest opportunity.

Such a situation as this cannot come just by chance. Some force or forces are obviously at work producing these results. What are these forces?

Overproduction. The reason for the situation just described is that all kinds of living things are capable of reproducing themselves at such rapid rates that there are always too many individuals on any given habitable area, to permit all, or even a small percentage of them to reach maturity. As pointed out in Chapter 11, overproduction and the consequent struggle for existence tends to select the better hereditary variations, and there is evidence that this action plays an important part in the production of new species. Likewise, natural

selection, which is effective because of overproduction, is probably responsible for many of the fine adjustments or adaptations of species to the environments in which they thrive.

In addition, *population pressures* result from the crowding effects of overproduction. As a consequence, there is a tendency to an outward movement of seeds or spores from every community, whether large or small. Much as the grains in a pile of sand become scattered in various directions by the action of every passing object, so propagules are driven from their sources into more or less distant territories.

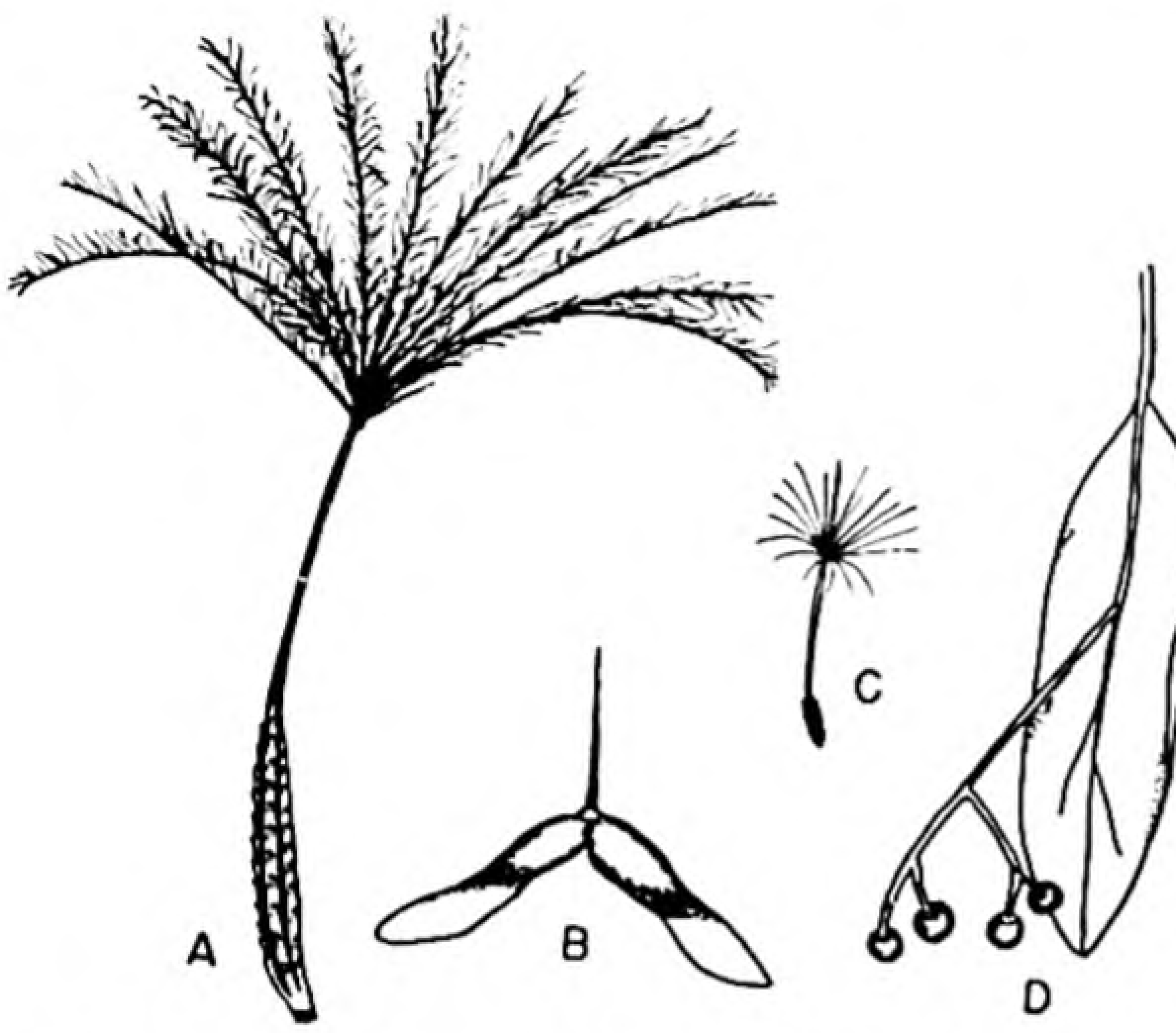
Because of this tendency to migrate, many kinds of organisms appear to rush in whenever there is a considerable reduction in the number of living things in a given locality. Therefore, any spot that becomes vacant in a location where life can persist, is soon occupied by one or more kinds of organisms.

Purple cliff brake growing high up on a vertical limestone cliff.

Dissemination. A high, sheer, bare, limestone cliff was left standing by the removal of stone from a quarry. Only a few years later there were hundreds of lichens, mosses and individual plants of a little fern, the purple cliff brake, growing successfully in patches scattered here and there over the rock face. How did these plants find their way into such inaccessible places? A knowledge of the life history of each of them gives the main outlines of the answer. Without much question, the dust-like spores of the ferns and mosses were carried by the wind and were deposited by chance in little irregularities in the rock. Slight accumulations of soil carried in as dust by the wind or by trickling water from rain or melting snow provided a sufficient combination of necessary chemical elements, and the spores grew. Those of the ferns developed into prothallia that formed gametes; these united and became zygotes; and the zygotes grew and organized the leafy fern plants. The spores of the mosses germinated and formed protonemata, which gave rise to

the moss plants. The lichens probably reached this rock wall as soredia, which had only to grow to become mature.

The scattering of propagules of any kind, whether they are spores, seeds, fruits, rhizomes,



Wind-carried fruits. (A) Salsify. (B) Maple. (C) Dandelion. (D) Linden.

gemmae, or other structures, is called *dissemination*. Obviously, the formation of well-defined communities such as occur almost everywhere, could not take place without the dissemination over considerable or even great distances of the various propagules from many species of plants.

Seeds and spores are usually much better fitted to being transported than the plants that produce them. They are small and compact and owing to dormancy may live for considerable periods of time under conditions of temperature, moisture or darkness that would quickly kill a vegetative plant.

There are many features in plant reproduction that favor dispersal of the offspring into distant areas. Some bring about a more or less haphazard scattering of the spores, soredia, or seeds while others cause dissemination to take place by means of highly specialized structures. In either case dispersal is often highly successful. In the following paragraphs are discussed a few of the more important and noteworthy forces that move propagules from place to place.

WIND. Some seeds, resting cells, soredia, and spores which have no features that especially adapt them to wind action are readily carried by air currents because they are small and light. Good examples are the seeds of mustard, evening primrose, mullein, poppy, and purslane. The smaller an object, the more easily it can be carried by the wind. This is due to the mathematical principle that if a piece of matter of definite shape increases in size, its volume increases more rapidly than its surface. That is, the weight becomes greater more rapidly than the surface on which the wind can act. An acorn is probably made of no heavier material than a mustard seed, but the wind is much more effective in carrying the latter. For the same reason, spores, being extremely small, can be transported by the wind for hundreds of miles without losing their vitality. In fact, cultures of many kinds of fungi have been collected by means of airplanes high above the surface of the earth.

FRUITS WITH WINGS AND PARACHUTES. Fruits that have wings or keys are called *samaras*. The wings of the samaras of such trees as maple, ash, and elm are broad extensions of the ovary wall which greatly enlarge the surface on which the wind can act without materially increasing the weight of the fruit. These fruits glide about in the wind as they fall and even after reaching the ground they are easily caught up again and carried along.

A far more efficient means of dispersal occurs in such achenes as those of dandelion, lettuce, thistle, and salsify. The pappus on one of these fruits acts as a parachutelike float, and under favorable conditions is sufficiently buoyant to carry the achene many miles, even a slight breeze sustaining it almost indefinitely.

TUMBLEWEEDS. Another extremely effective method of scattering seedlike fruits is that of the tumbleweeds, which are especially abundant in sandy places in the broad, flat plains.

There is a considerable number of species of tumbleweeds, including certain grasses, the Russian thistle, *Salsola*, the tumbleweed amaranth, *Amaranthus*, and winged pigweed, *Cycloloma*. All of these plants grow into a nearly spherical form and when they are mature they break off at the ground when they are shaken about by the wind. Thus freed from their attachment they go bouncing

across the country, carried by the wind, scattering their fruits far and wide. Under conditions especially favoring growth, the larger species, such as *Cycloloma atriplicifolium*, become 3 or 4 ft. in diameter. All tumbleweeds produce remarkable numbers of fruits.

WINGED SEEDS. Winged seeds play the same part in the distribution of species as winged fruits. The only essential difference is that the parachutes are outgrowths of the testa in the case of seeds, while they develop from the ovary wall in fruits. Examples of plants with winged seeds are milkweeds, fireweeds, cottonwoods, willows, pines, hemlocks, and cotton. In the case of the cultivated cotton, the fibrous floats are so greatly overdeveloped that they do not act as means of dispersal, but rather are harvested as soon as they are ripe, to be used commercially. Doubtless the seeds of the wild ancestors of cotton were scattered somewhat like those of milkweed.

WATER. Some seeds and fruits are light enough to float, while others that are too heavy can be rolled by running water. Those which are not readily carried in either of these ways may often be transported in masses of floating debris. The great variety of plants along stream banks and in areas subject to overflow, can be partly attributed to the effectiveness of water as an agency of dispersal, although credit must be given also to the fact that such localities, because of good soil and ample water, are naturally suitable places for plants to grow. In open flood plains such annual weeds as cockleburs and horseweeds frequently make extremely dense stands, their fruits being deposited in the mud at times of high water.

In lakes and ponds, water and wind may work together in scattering seeds, as can be seen readily by watching the drift of the minute achenes of cattails or the boatlike lotus fruits. The presence of seedlings of these plants along the shores proves that this is a successful means of dispersal. The seeds of many kinds of plants die, however, in a short time if they become water-soaked, and the fact that they are seen floating should not be taken as a proof that they will grow.

ANIMALS. Many kinds of insects, birds, and mammals are efficient and versatile agents of dispersal. When fruits are eaten, the seeds often pass through the alimentary tract uninjured. They may even be benefited by the softening action of the digestive juices on their outer coats. Even when animals store seeds, there is a good chance that

Tumbleweeds. (*Top*) Mature plant of *Cycloloma*, showing broken stem where the wind had detached it from its roots. (*Bottom*) A field of *Cycloloma* in sandy flood plain of Arkansas River near Hutchinson, Kansas.

some will be dropped and lost, or hidden away where they will never be found again. In this way the animal may unwittingly propagate the plants that will supply food to succeeding generations of its own kind. The maturity of fruits is closely correlated with this method of dispersal, for most of them, especially the fleshy ones, are less conspicuous and less palatable before maturity than they are when the seeds are ready for distribution.

Animals with wool, fur, or long hair become the unintentional carriers of burs and sticktights which they usually remove or lose far away from the place where they became attached. Some burs have spines that are sufficiently sharp and rigid to penetrate the skin of the animals and are carried in that way.

Water birds are very efficient distributing agents of aquatic plants. Resting cells and zygotes of algae, and the small seeds of such hydrophytes as cattail (*Typha*), pondweed (*Potamogeton*), and the sedges are frequently embedded in the mud on the feet of wading and swimming birds. During migrations, when they are traveling from pond to pond, they almost certainly transfer these propagules in large numbers from one of their resting places to the next. This habit probably largely accounts for the fact that numerous species of water plants are distributed over remarkably wide areas, even when the lakes and ponds in which they grow are completely isolated from one another.

MAN. Although man is an animal, he is in a class by himself as an agency that scatters plants over the surface of the earth. He not only makes longer journeys than almost any other living thing, but takes more materials with him and becomes the intentional or unintentional carrier of all kinds of seeds and spores.

Plants grown for foods, ornament, medicine, fiber, wood, or other purposes are taken wherever there is the remotest possibility of growing them successfully, and with them go weeds. The packing composed of straw, chaff, or similar materials, in which many things are shipped, the bedding for livestock on trains, road-building materials, ballast for stabilizing ships, refuse hauled away from the streets and alleys of cities, and many other objects transported from place to place, offer good opportunities for the scattering of seeds and spores. For this reason, exotic species are especially common along highways and railroads.

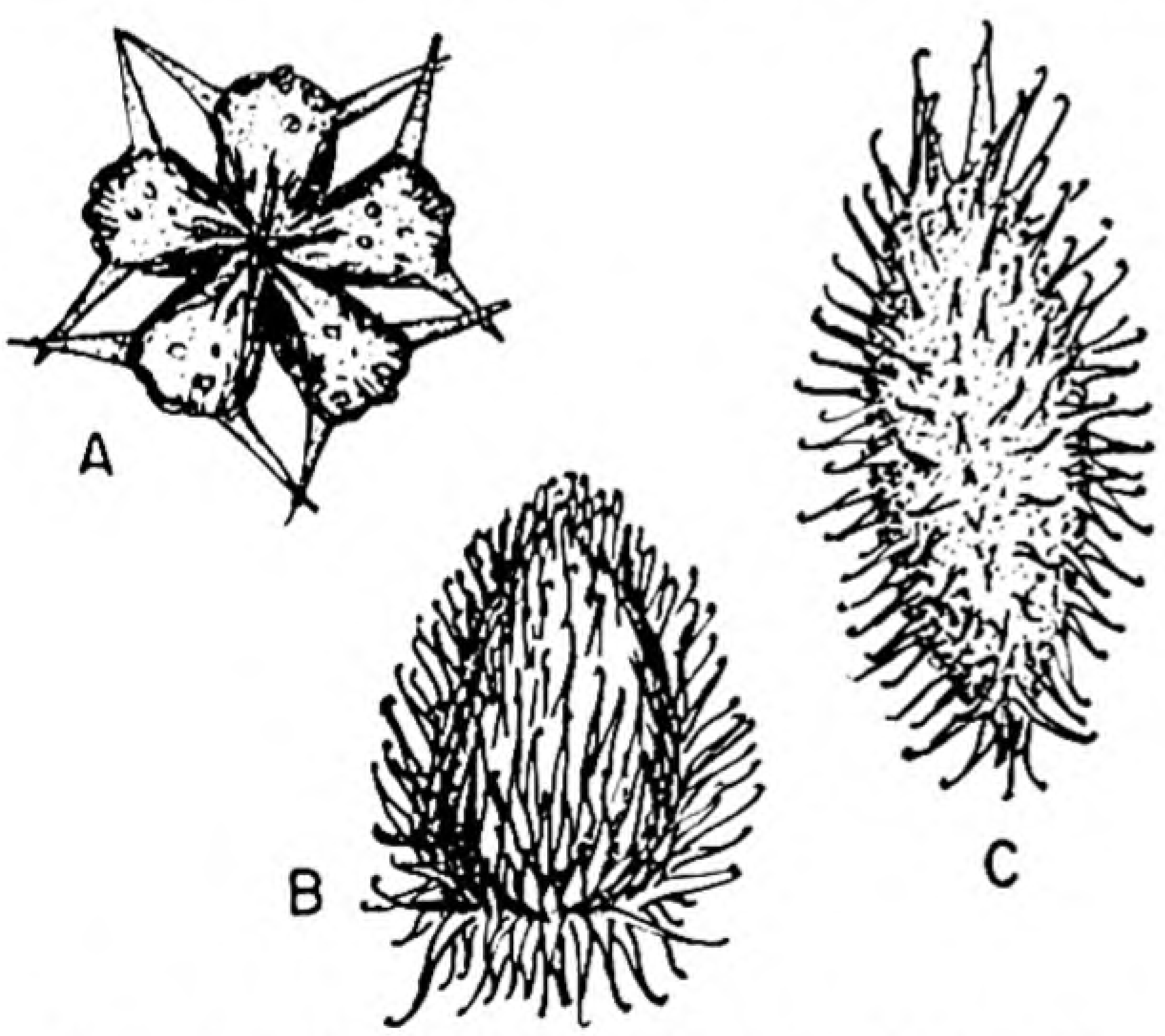
Seeds with parachutes. (A) Capsule (boll) of cultivated cotton containing seeds. (B) One seed with its fibers. (C) Seed of milkweed.

MECHANICAL DISSEMINATION. Some of the most highly specialized and most peculiar mechanisms of dispersal are those which are incorporated in the very structure of the seed or fruit. Some of these scatter seeds rather effectively, but it should be recognized that they are usually more spectacular than important to the plant, because only occasionally do they drive the seeds far enough away from the parent to carry them beyond the effects of its competition.

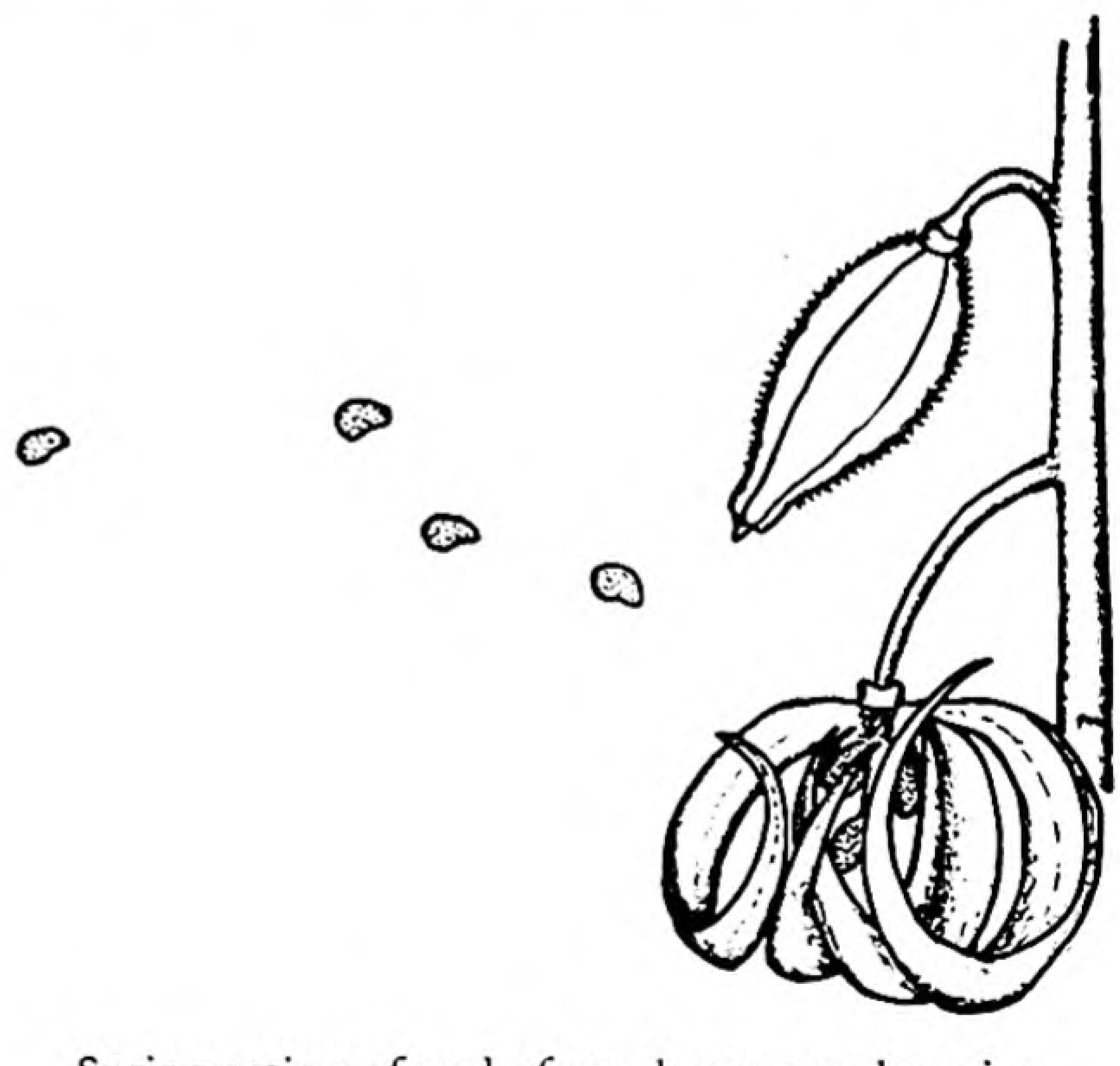
ELASTIC TISSUES. As the fruit of some plants matures and becomes dry, stresses are established in its walls by the unequal growth or shrinkage of different parts in such a way that each section of

Fence row with trees and shrubs planted by animals, probably largely birds, that dropped the seeds. The most prominent woody plants in this view are hackberry, wild black cherry, raspberry, blackberry, Virginia creeper, poison ivy, wild rose, elderberry, grape, and dogwood. Near Lafayette, Indiana.

the wall becomes something like a spring under tension. A slight disturbance is enough to start the opening of the pod, and the process is finished with a sudden snap as the springs are released. The seeds are frequently so attached that they are thrown short distances.



Burs. (A) Puncture vine. (B) Burdock. (C) Cocklebur.



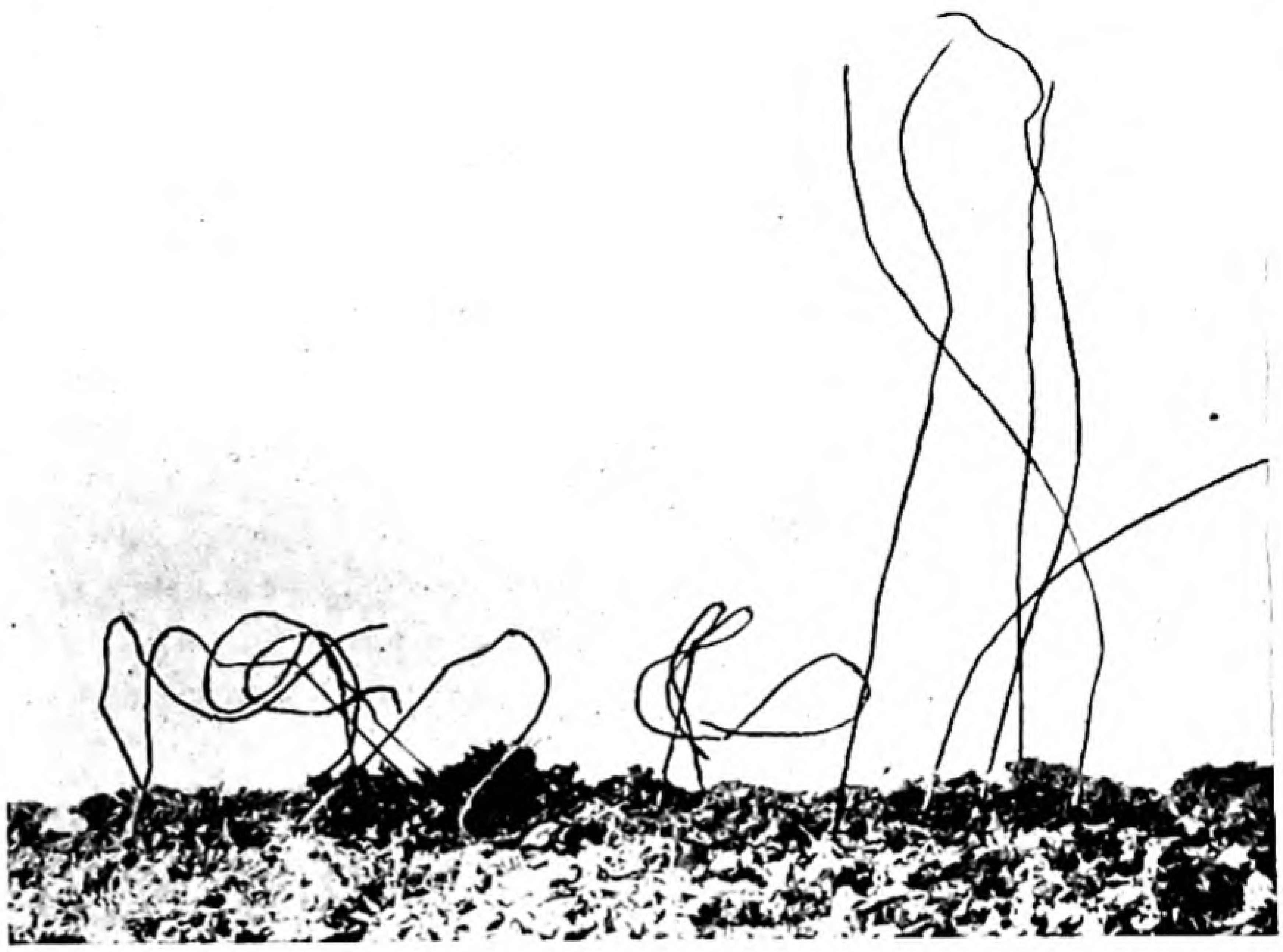
Spring action of pod of touch-me-not throwing seeds.

Some kinds of beans and many other species of leguminous plants have fruits which behave in this way, each half of the pod twisting with a jerk as it splits. This characteristic is more pronounced in the beans which have tough, fibrous hulls than in the more succulent and brittle kinds.

As the fruit of some varieties of castor bean dries, each of the three one-seeded carpels pops off the central core and jumps a short distance. Sometimes the pod breaks open at the same time, and an elastic spring of tissue flips out the seed. In this way it is often thrown 4 or 5 ft. from where it

would have fallen if gravity had been the only force acting upon it.

In the fruit of the wild geraniums each of the five carpels bears one seed at its lower end, the upper parts of all of them being united into the beaklike structure which has given to these plants the common name "crane's-bill." At maturity the outer wall of each carpel remains attached at the top but breaks loose at the bottom and coils up, usually throwing the seeds some distance. In somewhat the same manner, the capsule of touch-me-not breaks with a sudden snap, driving the seeds a short distance away. If the mature fruits of witch hazel are removed from the plant and allowed to dry in a large room, some of the seeds may be thrown as far as 30 ft. when the fruits burst.



Self-planting grains of *Stipa*. (*Right*) Grains just dropped into the soil, the awns still almost straight. (*Left*) Awns drying and twisting.

A variation of these springlike catapults follows the same principle as that employed when a watermelon seed is "shot" from between the thumb and finger. The violet illustrates this type. In this plant the fruit splits into three boat-shaped parts which remain attached to the receptacle, and the edges of each of these press inward, forcing out the smooth, hard seeds. In the oxalis, specialized pads of elastic tissue, probably outgrowths of the placenta, accomplish the same results when the fruit splits open.

TURGIDITY. Some fruits become so distended with water as they mature that they burst explosively, scattering their seeds and pulp. This action may be as simple as a large, pulpy fruit with a tough rind falling from a tall tree, or it may be more specialized as in the "squirting" cucumber. The fruit of this plant is in the form of an elastic bag filled with pulp and seeds under pressure. The receptacle fits in one end like a stopper in a bottle, and, when the fruit falls off, the contents are squirted out.

HYGROSCOPIC TISSUES. Many plant structures change their shape because of the unequal swelling or shrinkage of different parts as they absorb moisture or lose it. Among the most active organs of this type are the long, bristlelike *awns* attached to the grains of many grasses. These tend to be straight when moist and variously twisted, coiled, or bent when dry. As the awn becomes alternately wet and dry while lying on the ground, the changes in the shape often cause the grain to move about in peculiar ways.

A striking example is that of the fruits of such grasses as *Heteropogon* and *Stipa*, which even plant themselves under some conditions. At one end each has a long, hygroscopic awn and at the other, a hard, sharp point known as a *callus*. When the fruit falls from the plant, the awn, acting like the feather of an arrow, causes it to stand on end with the callus on the ground, the entire structure being supported by surrounding objects such as weeds and grasses. When the awn is wet, it straightens, but, as it dries, it first bends at right angles, and then the lower part twists, causing the callus to bore its way for a short distance into the soil. If the awn now becomes wet again, it first untwists and then straightens, and a second drying causes the callus to bore a little deeper. The effectiveness of this mechanism is seen in the fact that seeds of

some species are sometimes planted in this way to a depth of more than an inch.

VEGETATIVE PROPAGATION. A few of the more obvious active agents that carry propagules from place to place by mechanical means have been discussed in previous paragraphs. These various agencies are often very efficient in transferring a species from one region to another, because many of the seeds and spores travel long distances. For this same reason the wastage is immense, because few of the myriads of the propagules happen to fall into a spot suitable for their development.

In contrast, many plants produce runners and rhizomes that effectively extend the area they occupy. Strawberries, white clover, Bermuda grass, and cinquefoil are well-known examples of plants that enter new territory by means of runners that form adventitious roots at frequent intervals, while most of the sod-forming grasses, the cattails, and many ferns have rhizomes that branch extensively underground and greatly increase the numbers of aerial shoots. A few species reproduce themselves by sending up shoots from widely spreading horizontal roots. Some of the wild plums, many of the sumacs, and the silverleaf poplar frequently make thickets in this way. Sometimes the young plants crowd so close together that they almost completely control the area in which they are growing because few other species can withstand their dense shade.

While these means of migration into new areas are relatively slow they are correspondingly certain, because the young plant is firmly attached to its parent until it is thoroughly established. Although a plant with rhizomes or runners can extend its range only a few square inches per year, it may spread into much new territory in the relatively short span of a century.

SURVIVAL AFTER DISPERSAL. The fate of a propagule after it reaches the end of its journey is important. Many seeds make only the initial trip after leaving the parent plant, while others may be picked up again and again by various agencies during the dormant season, and carried here and there before reaching a final destination. Although little is known of how adaptations came about, some agencies of dispersal are probably a little more directive than mere chance but almost all of them are as aimless as the wind itself, and while many seeds reach locations favorable for growth, most of them arrive in places where they have not the slightest chance to produce successful adults.

In almost any place one may choose for study, every gradation in adjustment can be found from absolute inability of certain species even to begin growth, to the ready establishment of others. By a variety of natural processes, the various means of propagation of great numbers of species of plants are deposited every year in any given locality.

An intensive study of all the propagules reaching a pond at any place in the upper Mississippi Valley, as an example, would reveal those of many species of algae, fungi, bacteria, liverworts, mosses, ferns, and seed plants. Of these, relatively few kinds grow and reproduce themselves. The rest die. To be more specific, the acorns of white oak and the seeds of willows may fall into the mud at the margin of the water. If the acorn germinates at all it dies very soon but the willow seeds find themselves in conditions ideal for germination and continued growth. If, however, these same seeds had fallen into the leaf mold in a grove of trees on higher ground a few rods away, the oak might have grown normally while the willow would have died for want of water, without even germinating. Such facts as these can be observed by any one who will look for them in almost any locality.

Stated in another way, plants of different species are so constructed because of their hereditary traits—their combinations of genes—that they can live in certain types of environment but not in others. Each environment, therefore, limits the kinds that can grow in it. Overproduction tends to cause migrations into new territories and the various phases of environment determine which of the immigrants can become established and reproduce themselves.

In this way, a given type of environment tends to cause the development of a relatively uniform aggregation of species. The activities of these species usually become coördinated to such a degree that the entire group behaves as if it were a unit under the control of the dominants. Such group activity usually brings about considerable

changes in the environment. Humus is produced, shade is usually cast by members of some of the species, and the amounts of available water in the soil and the relative humidity of the air are altered. The environment exerts a selective effect on the association, and the association, in turn, changes the environment.

Within any well-organized association every organism is subjected to intense and intricate stresses by all its crowding neighbors. Such crowding of plants and animals, as well, is sometimes referred to as *biotic pressure*. It is through this pressure that the excessive numbers of individuals that are given life by their parents soon lose their lives, furnishing food for bacteria or fungi of disease or decay, thus adding their bit to the fertility of the soil.

Not only do these biotic pressures bring about the destruction of many individuals in every community, but they exert constructive effects as well. They are the forces which crowd organisms together into a compact association in which the life processes of each individual act as a set of checks and balances on all the rest. And the very compactness of these communities often adds greatly to the success of the individual species composing them. As examples, successful pollination in many plants is much more certain if the individuals are near together than if they are widely scattered. Likewise, fertilization in most of the algae, fungi, bryophytes, and other lower plants can seldom occur unless the male and female gametes are produced so close together that the microscopic sperms can swim to the eggs.

SOME ASSOCIATIONS IN THE UNITED STATES

There are numerous plant associations which can be recognized within the borders of the United States. A few representative ones from rather widely scattered parts of the continental portion of this country will be discussed.

In the more northerly parts of the eastern United States the most characteristic of these are the sugar maple-beech and the oak-hickory associations; in the southerly, warmer portions east of the Mississippi River, these give place to a number of other communities, such as the southeastern coniferous forest dominated by longleaf, shortleaf, and loblolly pines. In swampy places the bald cypress-tupelo association is common.

Occupying a vast area to the west of these eastern forests are the grasslands, most distinct of which are the tall-grass prairies at the western margins of the forests, and the short-grass association which continues on to the Rocky Mountains. In the West and Southwest beyond the grasslands, much of the area is divided between such coniferous forests as the ponderosa pine, and the dwarf, piñon-juniper association, on the one hand, and several more or less definite desert scrub associations such as sagebrush or creosote bush, on the other.

Of the numerous associations that are known, only a few will be discussed to illustrate the more extreme types.

Sugar Maple-Beech Association. To one entering a maple-beech forest that is in full leaf, the usual impression is that of a high-vaulted canopy made up of the close-fitting crowns of the trees, supported by their straight, tall, columnar trunks. Living with them usually are scattered representatives of other tree species such as red maple, linden, white ash, yellow birch, and tulip tree.

The maple-beech forest casts such a dense shade that the undergrowth of shrubs and small trees is limited to scattered individuals that have extreme ability to withstand greatly reduced light. A few of these shade-enduring species of smaller woody plants are flowering dogwood, witch hazel, and serviceberry.

In early spring, before the dense crown of leaves has developed, there is usually a remarkable display of such wildflowers as violets, trilliums, May apple, spring beauty, bloodroot, dog-tooth violet, Jack-in-the-pulpit, anemone, columbine, geranium, and phlox. By midsummer most of these plants have shed their seeds and are withering down to the ground.

Associating with the rest, frequently, are numerous species of ferns, lycopods, and mosses. Fungi, large and small, are to be found in immense num-

bers, bringing about the decay of the fallen leaves, dead stumps, and logs.

All the plants of this association have remarkable powers of reproducing themselves in dense shade. Species such as the aspens, fireweeds or most of the grasses, that require a great deal of light, are automatically eliminated. On the other hand, the seedlings of the beeches and maples can live for long periods of time in a surprisingly small amount of light. This association is the climax in the region where it has developed, because the young plants are able to survive in the conditions that are established by the growth of their parents. This makes a stable and permanent association.

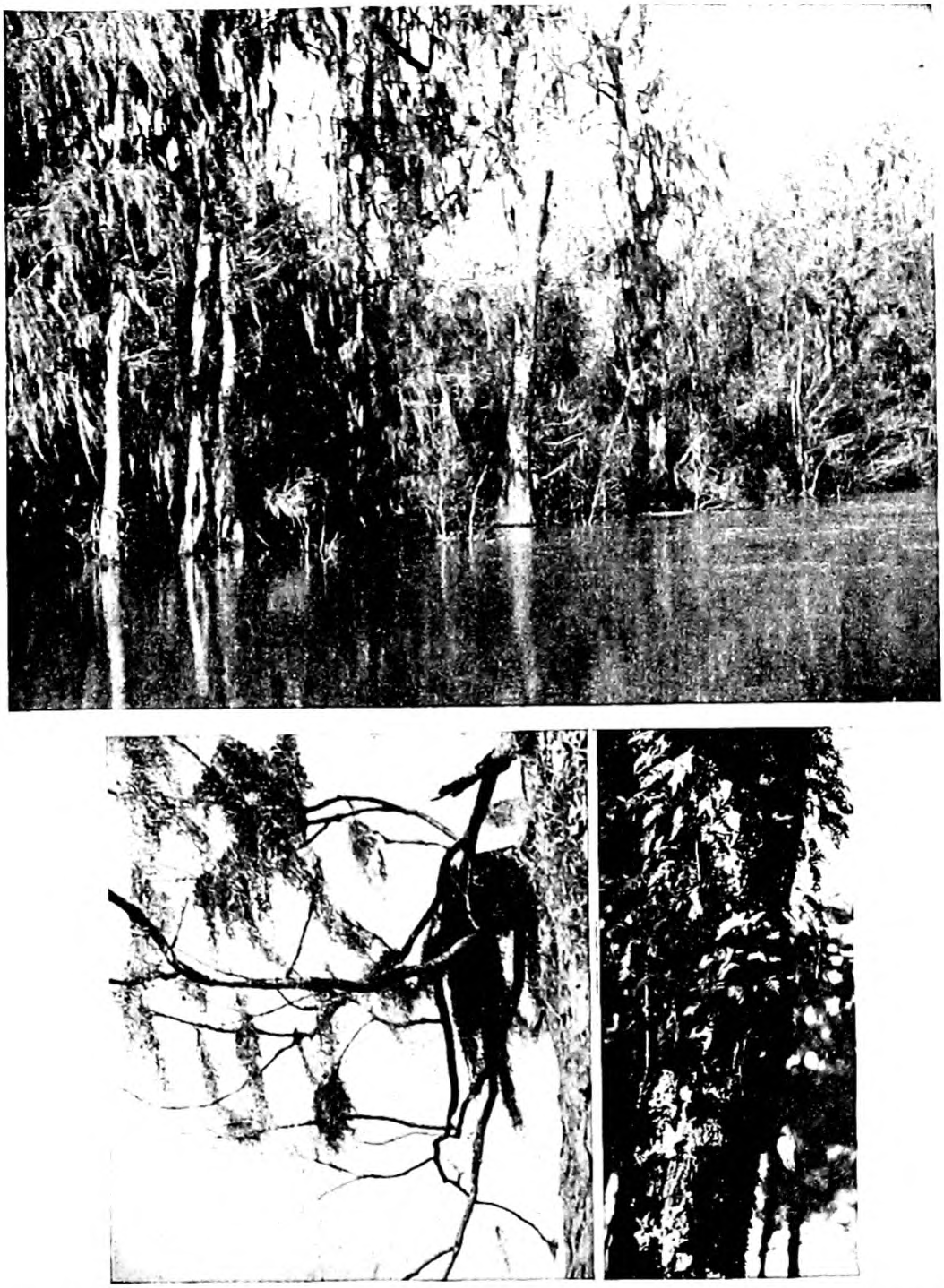
Deciduous forests are limited to regions where there is sufficient rainfall to keep the soil moist throughout the year and where there is ample precipitation in the winter to maintain a fairly high humidity while the trees are dormant. The reasons are self-evident, because trees with their roots in cold or frozen soil are unable to absorb water and replace that lost by transpiration during the winter. Therefore, extreme dry winds, such as those encountered in the grassland climates, prove to be very destructive to the greatly exposed parts of tall trees.

Maple-beech forest association. Southwestern New York. (Courtesy, New York State Museum.)

Oak-Hickory Association. The lines between this association and the last are not always clearly defined, for in some places oaks and hickories occupy the drier, more exposed areas in the maple-beech association; likewise, beeches and maples are often successful in oak-hickory communities.

The slightly greater dryness of habitat occupied by the oaks and hickories does not always result from a lack of rainfall. Even in the northeastern United States, in places where climatic conditions would permit the development of the maple-beech association, south-facing slopes that are extremely well drained or sterile, and sandy soils in which beeches and maples are not successful, are frequently covered with oak-hickory forests.

In addition, the oak-hickory forest forms an irregular zone in a westerly and southwesterly direction from the main body of the maple-beech association. This zone occupies an area in which the general climatic conditions are much the same as those in the East but in which annual precipitation is distinctly less. Long tongues of this forest extend far westward into the drier grasslands, in the more humid strips along the rivers.



Bald cypress-tupelo association. (*Bottom*) Close-up views of Spanish moss and epiphytic ferns and lichens. Southern Louisiana.

The oaks and hickory trees, in contrast with the beeches and maples, do not form a closed, continuous crown and therefore do not cast an extremely dense shade. In this more open plant community a tangle of undergrowth is characteristic, made up of light-requiring shrubs and small trees such as blackberries, hazelnuts, and redbuds.

Bald Cypress-Tupelo Association. This community is to be found in extensive shallow swamps and sluggish streams in the southern and south-

Bald cypress-Tillandsia association. (Courtesy, Clair A. Brown, Louisiana State University.)

eastern part of this country. The association is characterized by close growths of trees casting a dense shade with breaks in the crown where water is deep or is flowing. In addition to the two dominants, bald cypress, *Taxodium distichum*, and tupelo, *Nyssa aquatica*, there are considerable numbers of such trees as red maple, white cedar, and black gum. In places where the water is only a few inches deep or where the wet soil emerges from the water and where sufficient light penetrates to the ground there are almost impenetrable jungles of shrubs. Likewise, among the shrubs, and extending out into the deep water, are many species of herbaceous plants, such as iris, coarse grasses, rushes, bulrushes, sedges, and water lilies.

The trees that grow in these great swamps usually form expanded, cone-shaped "buttressed bases" and the peculiar knees of the bald cypress have been described in an earlier chapter. Many kinds of epiphytes grow on the branches, in crotches between the larger limbs, and on the cypress knees. These epiphytes include, besides small plants like mosses, liverworts, and lichens, such larger forms as ferns, orchids, and pineapplelike bromeliads, that send out a tangle of roots and rhizomes extending through and over the bark of the tree trunks. In addition, hanging from the branches everywhere are picturesque drapes of Spanish moss (*Tillandsia*).

The soil is largely a thick spongy, poorly disintegrated peatlike layer made up of dead leaves, branches, and fibers in which organisms of decay are not active.

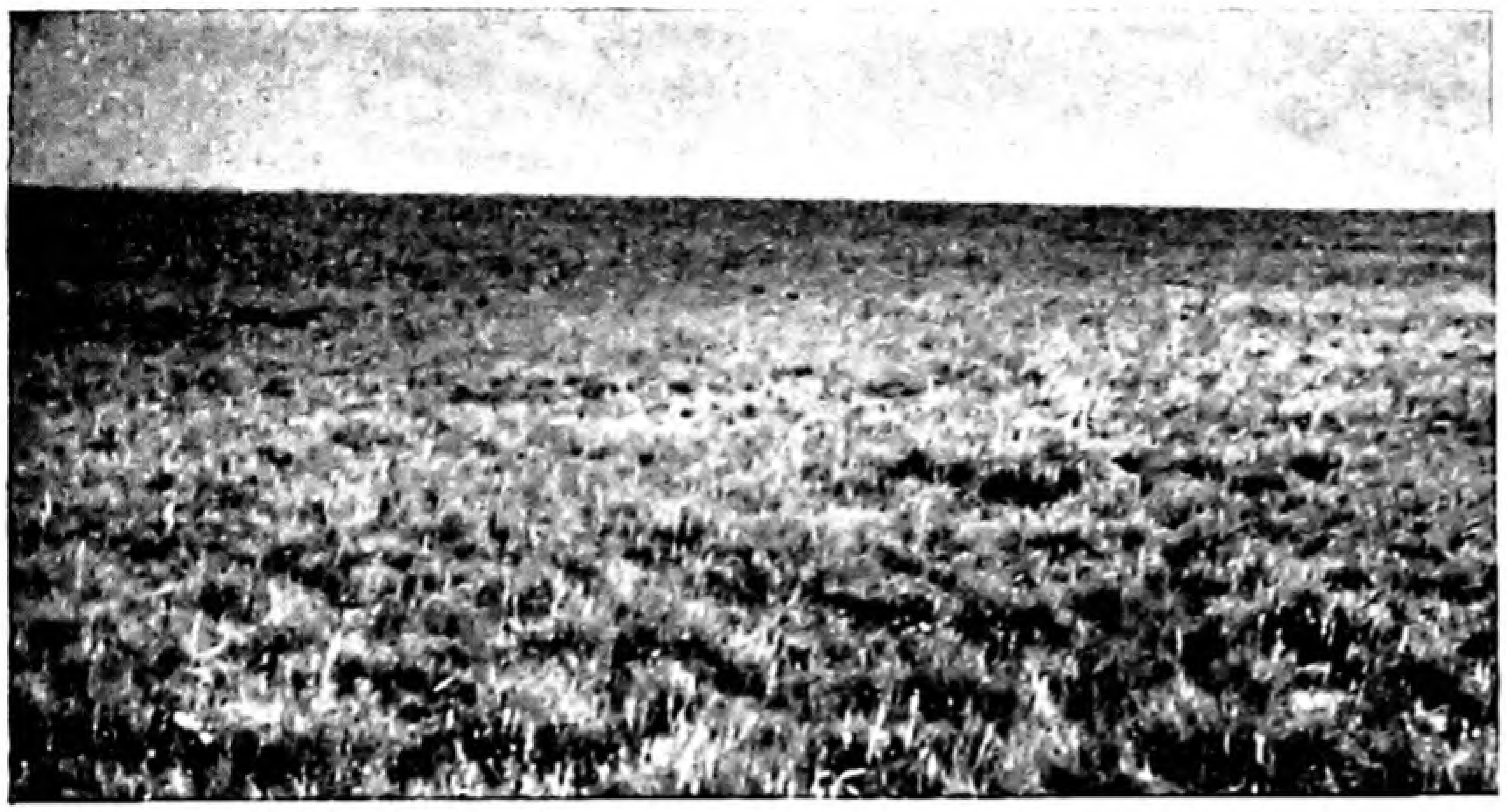
The almost odorless and tasteless coffee-colored water of these swamps is the home of large numbers of animals such as wading and swimming birds, the alligator, water moccasin, and many kinds of frogs and mosquitoes, and on the higher portions where the ground is not so wet such wildlife as deer and bear abound.

This association is in no sense a climax. Instead, it is only a step in the sere in which much humus is being produced, gradually adding to the soil and filling the depressions.

Ponderosa Pine Association. In contrast with the associations of humid climates or in swamps, the western yellow pine forests occupy relatively dry locations in the western United States. This association takes the form of widely spaced trees, often with little undergrowth except a few lichens, mosses, small grasses, and occasional shrubs. In places where rainfall is somewhat greater, Douglas fir trees often become a part of the community.

In this association the young pines usually grow somewhat distant from the large parent trees. In places where the adults stand far apart, the seedlings commonly form an irregular zone around each of them. The young trees are unable to estab-

Ponderosa pine association. Northern New Mexico.



Short-grass association. Northern New Mexico.

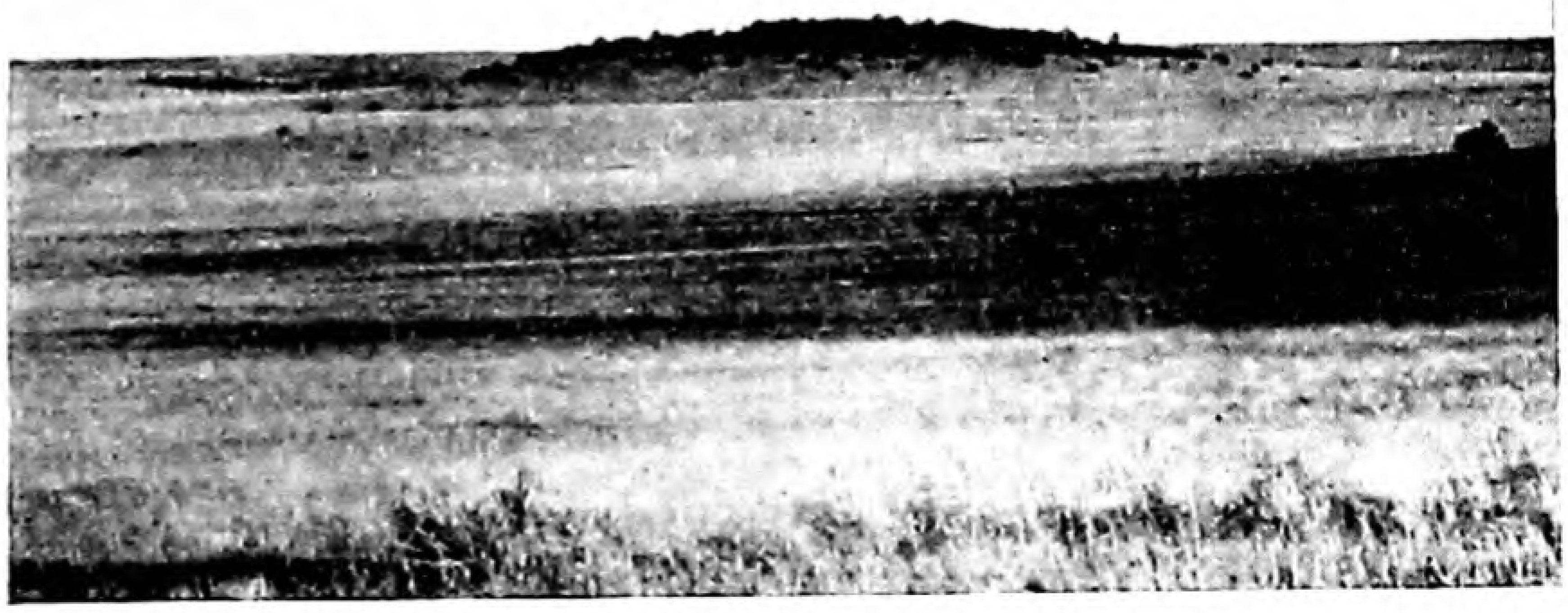
lish themselves directly under the mature ones. Experiments have shown the reasons. These pines have two distinct sets of roots. One set is vertical, growing deep into the ground, and the other extends horizontally, only a few inches below the surface. After a rain, the horizontal roots quickly absorb the moisture from the superficial layers of the soil, making it impossible for seedlings to gain a foothold.

One other factor plays a part in maintaining the characteristic open stand of the ponderosa pines. They are very sensitive to shade. Even in places where the seedlings are somewhat crowded together many of them die because they cannot withstand the shade of their neighbors. Hence the combination of strong competition for both water and light produces a community of individuals standing far apart.

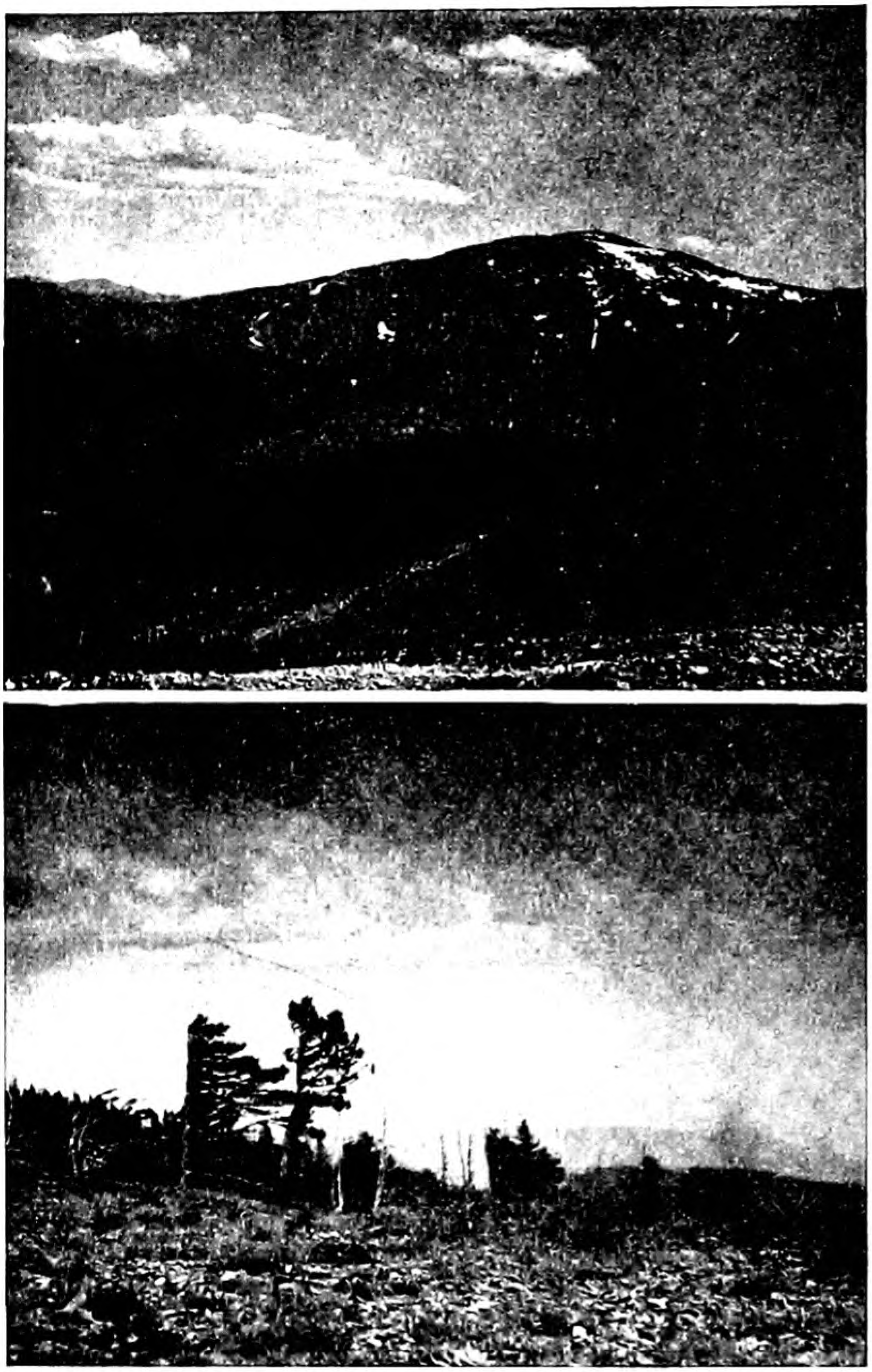
An almost universal member of the ponderosa pine association is the porcupine. This animal commonly damages occasional trees by gnawing the bark from their trunks high up near the top, causing abnormal branching and reducing the value of such trees for lumber. Two human activities have been found to be the causes of great increases in these losses. The first is heavy grazing. Not infrequently cattle, sheep, or goats are allowed to destroy almost the entire ground cover of these forests. When this is done the porcupine, which normally feeds to a considerable extent on small plants such as shrubs and grass and much less on bark, is driven by hunger to a diet largely of bark. Under these conditions, moderately large trees may be almost entirely stripped, causing their immediate death.

In one other way man is throwing the biotic community out of balance to his own hurt. A normal part of the ponderosa pine association is a small group of predators such as mountain lions and bobcats. These animals are seldom numerous, but they accomplish the important function of controlling the numbers of porcupines, rabbits, and other animals that sometimes tend to multiply too rapidly for the welfare of the total forest. In many places there has been an organized attempt, not to control but to exterminate these predators. The combined action of excessive grazing with the destruction of these natural checks and balances is slowly but effectively reducing the production of pine lumber.

Short-grass Association. There are few associations that contrast more sharply with the various



Tension zone between short-grass association in ordinary soil and piñon-juniper association in rocky place. Near Las Vegas, New Mexico.



Altitudinal zones in the southern Rocky Mountains. (*Top*) Line between forest and alpine mat plants and grasses. (*Bottom*) Nearer view, showing crippled trees at timber line.

types of forests just described than the short-grasses of the western part of the Great Plains. Probably not a single species native to the short-grass lands could be successfully introduced into any one of the forest associations of the eastern United States. Likewise, the species of the eastern forests cannot reproduce themselves in the short-grass plains, even though occasional individual plants may be caused to grow to some extent if they are planted carefully and given sufficient attention.

The forest climate is one that supplies moderate to high soil moisture and humidity of the air throughout the year. In contrast, the climatic conditions that lead to the development of grasslands are those in which most of the moisture falls during the growing season, with relatively little precipitation in winter. Grasses usually die down to the ground in winter and the rhizomes or other underground parts become dormant, and dryness of atmosphere and soil can have little effect on them. Trees, on the other hand, with their trunks and branches exposed to dry winds, are likely to be greatly weakened and even killed.

The short-grass association is as compact and well organized as any other community. In fact, the very closely matted roots are so efficient in absorbing water that the soil is usually dry below them and deep-rooted plants are seldom able to live. The dominants are chiefly various species of grama grass, *Bouteloua*, and buffalo grass, *Buchloe dactyloides.* Even under good conditions of growth these grasses seldom become more than 1 or 2 ft. tall during midsummer.

With the dominants there are usually considerable numbers of other small grasses together with numerous species of low-growing plants of various kinds, most important of which are members of the pea and composite families.

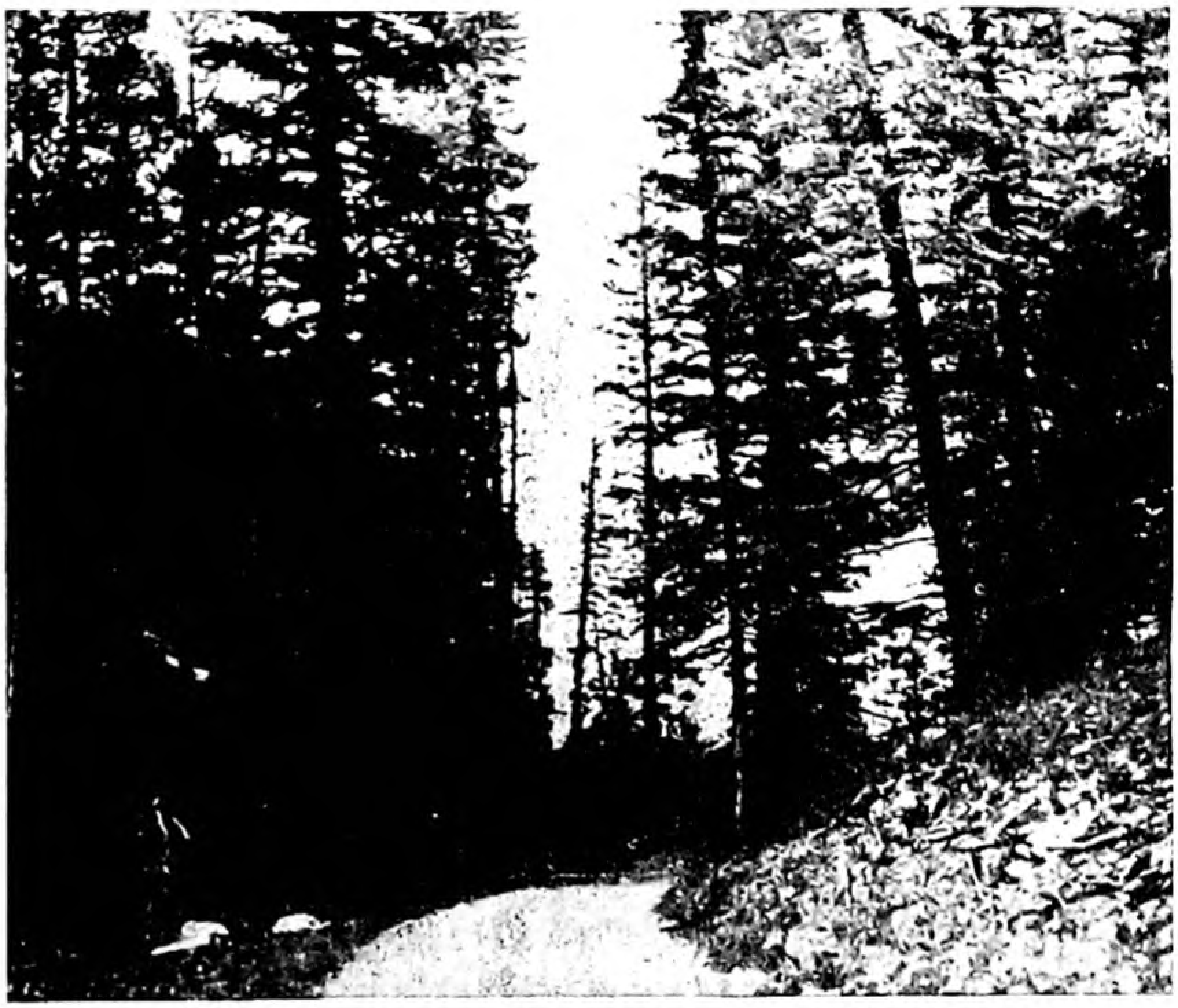
Tension Zones. One source of confusion to the student out-of-doors should be mentioned here. At those places where two associations meet, they commonly overlap. Therefore, some members of

each may be found within the bounds of the other, making a rather complicated situation. Sometimes these tension zones are many miles wide, with climatic conditions so nearly uniform throughout, that one association or the other may be in the ascendancy at a given place, depending on slight local differences in the characteristics of the soil, in the direction of slope of the land, or in the amounts of drainage.

As an example, in tension zones between the maple-beech and oak-hickory forests, mentioned above, the former frequently occupies all or most of the region, with the exception of well-drained south-facing slopes, or places that have been damaged by fire. Not infrequently the oaks and hickories form small communities in these drier or more exposed localities.

Even more striking is the tension zone between the short-grass associations of the Southwest and the dwarf woodlands of piñons (nut pines) and junipers, for the grasses are dominant in the better soils while the piñon-juniper association controls many of the rocky places where the grasses cannot succeed.

Zonation. In places where local conditions vary markedly in a short distance, clear-cut series of narrow zones often occur. Thus, around a shallow lake margin, definite zonation frequently appears, depending on the depth of the water and the wetness of the mud along the banks. In the open water floating algae and duckweeds are found. Toward the shore there often follow zones of water lilies rooted in the mud under a considerable depth of water; of bulrushes and cattails in the more shallow margins; of willows followed by cottonwoods on the wet banks; and finally of elms and silver maples merging into the upland forest. The zonation around a lake in the prairies is usually practically identical with that just described, with the exception that grasses largely replace the trees. The willow-cottonwood zone may or may not be present. In the short-grass region, as a rule, no zone of woody plants is to be found. (See illustration on p. 341.)



Altitudinal zones in the southern Rocky Mountains, lower elevations. Beginning above timber line (see illustration on p. 358), we descend to the humid evergreen forest in upper view here and to scrub oak and small evergreens in foothills, lower photograph. In the background lie the still drier short-grass plains.

Zonation often takes another form in mountains where one belt of vegetation succeeds another at different altitudes. Water is doubtless of great importance here because rainfall usually increases with altitude up to relatively high elevations on mountain slopes, although at still higher points there is often a marked decrease in available moisture. Other variables, such as temperature, winds, and character of the soil also probably play a considerable part. A mountain or a range rising out of a desert usually has a considerable zone of scrubby woodland above the desert proper, followed by open growths of trees that can live in moderately dry places, thence merging into a damp forest with its characteristic undergrowth of ferns, mosses, and other plants that require shade and moisture.

At exceedingly high altitudes with their combination of low temperature, reduced rainfall, and high winds, there develops a scrubby forest of crippled trees. Above this forest there may be a waste that is frozen much or all of the year. None but the most resistant plants can live here because absorption is impossible from frozen soil, and the driving winds, that are often extremely dry, tend greatly to increase transpiration. None but very small plants are able to survive under these rigorous conditions. The characteristic vegetation of such locations is composed of lichens, very low grasses and sedges, and minute woody plants that lie close to the ground, in places forming mats a few inches thick. These tiny plants are covered with snow during all but a brief summer period. Annuals are extremely rare because of the shortness of the growing season, for all growth takes place very slowly and few species can develop from seed, reach maturity, and form seeds of their own in the short time in which growth is possible.

Wherever a high mountain rises from humid surroundings the series of zones begins with the damp forest and continues upward in the same order as that described above.

Zonation may occur wherever there is marked gradation from one growth condition to another, as in the distribution of water from a pond to the shore; of rainfall at different altitudes on a mountain; of soil from gravel to rich humus; or of alkali or salty soil to that which is almost free from salt.

In closing this chapter it should be explained that it was Warming, the great Danish botanist, quoted in introducing this subject, who first set forth in well-organized form the concepts of plant communities as they were coming to be understood in the latter part of the nineteenth century. While he played a great part in developing the phase of botany known as Plant Ecology, rapid progress is still being made in this field. Consequently, it is now possible to go much farther than he did and study not only "the nature of the weapons by which plants oust each other from habitats," but to see more clearly the forces at work in such competition. In addition, it is now becoming evident that a very high degree of interdependence exists among the individual plants and between the plants and animals of communities.

SUPPLEMENTARY READINGS

Campbell, "An Outline of Plant Geography."
Clements, "Plant Succession and Indicators."
Daubenmire, "Plants and Environment."
McDougall, "Plant Ecology."
Oosting, "Study of Plant Communities."
Schimper, "Plant Geography on a Physiological Basis."
Warming, "Ecology of Plants."

Chapter 23

BIOTIC COMMUNITIES: CHECKS AND BALANCES

"A woodland climate leads to victory on the part of the woodland, a grass climate to victory on the part of grassland. In transitional climates edaphic influences decide the victory. Strong deviations from a woodland or grassland climate produce desert."

—SCHIMPER

Life processes play important parts in changing environment, but climate and other inanimate forces dictate the ultimate outcome. Some of these forces and their human significance are discussed in this chapter, as follows:

- Water
  - Hydrophytes
  - Xerophytes
  - Mesophytes
  - Water Balance and Plant Structure
  - The Meaning of Xerophytism
- Light
  - Light Requirement and Light Tolerance
  - Photoperiodism
- The Soil
  - Soil-forming Forces
  - Soil Composition
  - The Soil Profile
  - Root Systems and Water Supply
- The Living Environment
  - Social Symbiosis
  - Parasitism
  - Commensalism
  - Carnivorous Plants
- The Web of Life
  - Man's Relationship to the Web of Life
  - Plants as Soil Cover
  - Man and Erosion
  - The Remedy for Erosion
  - Aimless Destruction
  - Constructive Activities

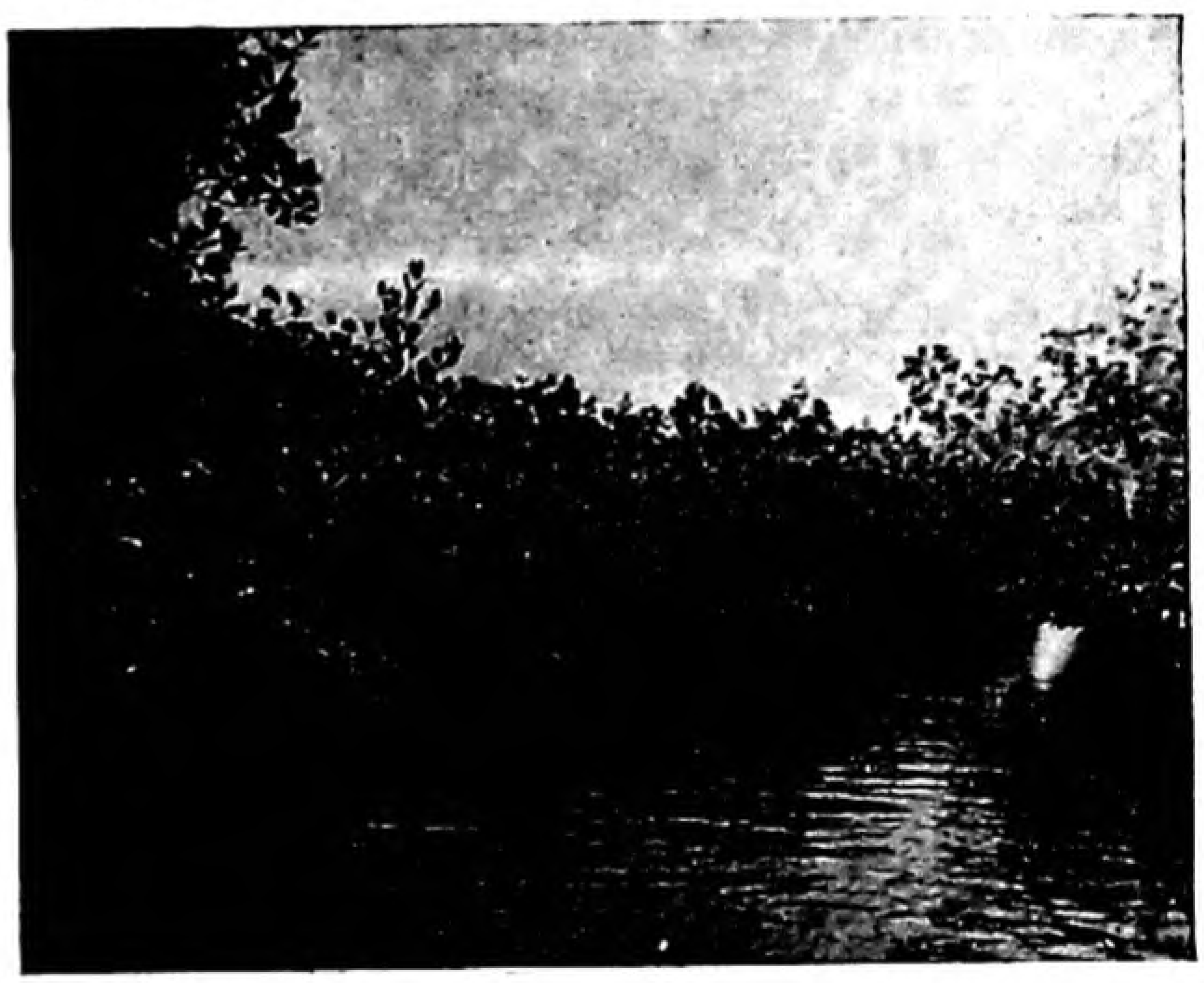
Man is like a fish in a balanced aquarium. If he should succeed in breaking the bowl he will be not the master he thinks himself to be, but food for bacteria. Then a new balance may become established in nature—a balance in which he will have no part. If, on the other hand, he can learn to be a part of nature's balance, success will be his.

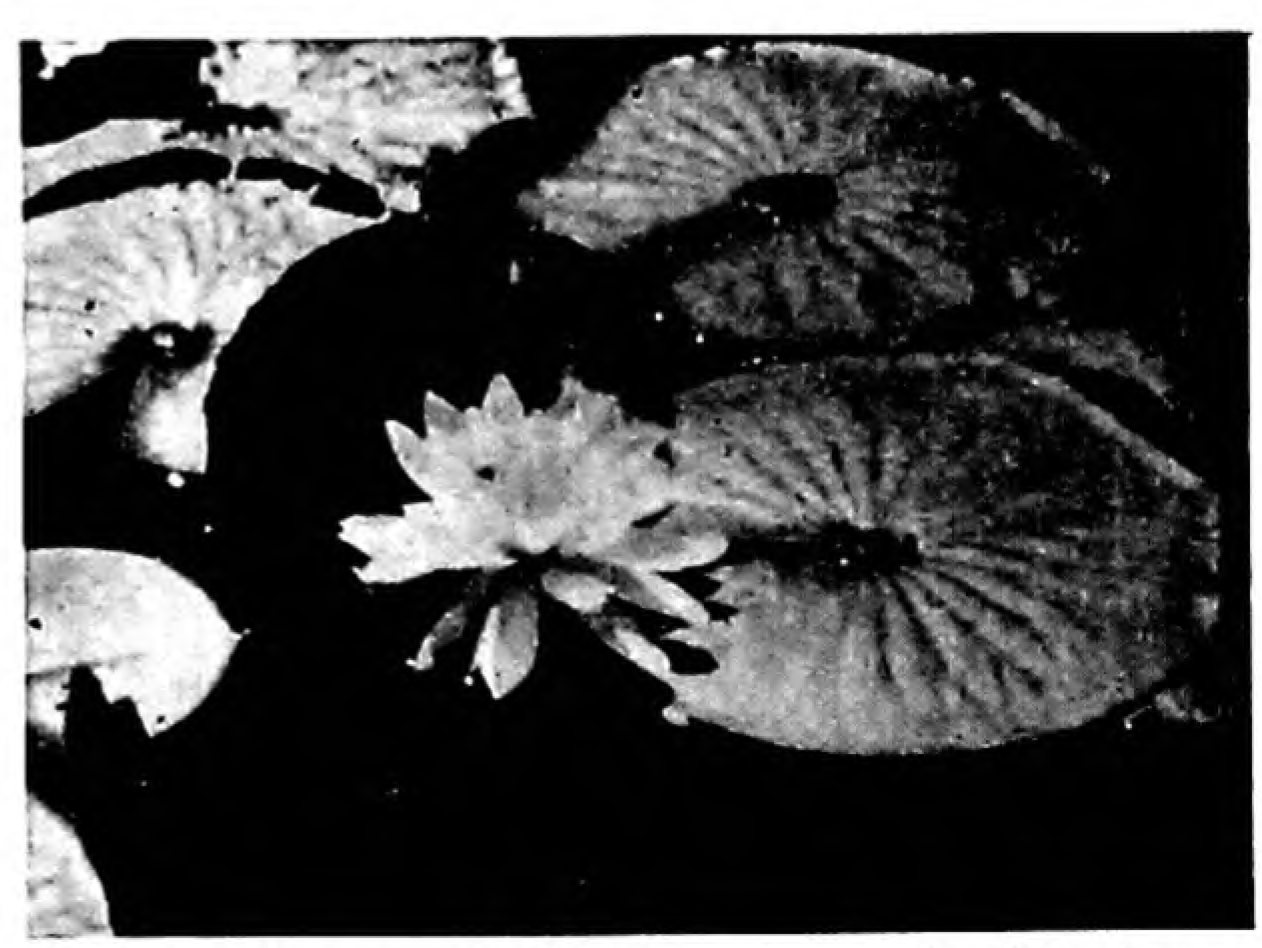
The last chapter developed the concept that each type of environment limits the kinds of plants that can grow in it. A detailed study will show, however, that environment is composed of many factors all of which play parts in controlling distribution and success of species. Some of them are physical, while others are biologic. Water supply, rate of evaporation, light, soil, and temperature are among the most important physical factors, while numerous effects of other plants and animals act as biologic controls. Water plays a fundamental part because it is necessary in all metabolism, while at the same time it tends to be lost by transpiration. Therefore, it is especially effective in setting limits to the distribution of species.

WATER

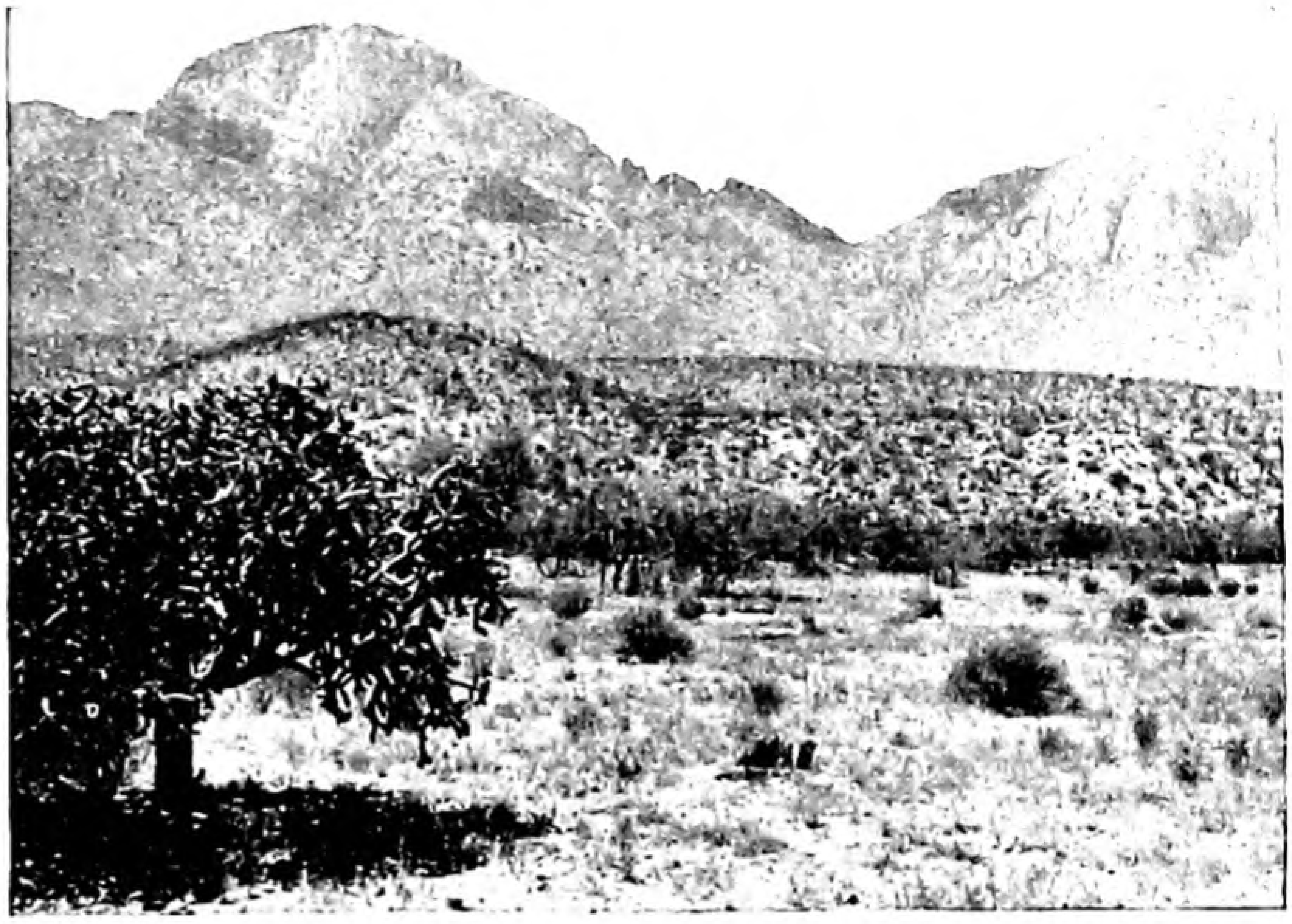
In order that a plant may thrive, enough water must be taken in to replace that which is lost in transpiration plus that which is used in all phases of metabolism. Whenever loss exceeds intake, wilting soon occurs, growth ceases, and, if this condition continues long enough, the plant dies. On the other hand, an excess of water reduces the supply of oxygen, hence many plants are unable to live submerged or with their roots in extremely wet soil. Because water holds a very important place in the life of plants, and because of the great variations in structure and physiology by which they are adjusted to it, plants tend to form communities rather definitely related to the one factor of water. On this basis they have been grouped roughly into three general categories, *hydrophytes*, *mesophytes*, and *xerophytes*.

Hydrophytes. These are plants that grow with a part or all of the body in mud or water (*hudor*, water; *phyton*, plant). Under such conditions they have an excess of water and are usually protected by their surroundings from much or any danger from transpiration. Even when they are exposed to such danger because the pond or swamp in which they live dries up, submerged parts do not have the capacity to produce coatings of cutin or cork or otherwise to protect themselves from drying. Such plants usually die very soon when removed from the water. On the other hand, these same cell membranes which freely permit transpiration, are, for the same reason, effective absorbing surfaces as long as they remain submerged. Plants that are amply supplied with water and are not subjected to excessive transpiration are said to have a *high water balance*. This expression is an apt figure of speech that refers to a bank balance with its income and outgo; if income is great and expenditures small the balance is high. *A hydrophyte, then, may be defined as a plant with a high water balance.* Examples of hydrophytes are the many species of floating algae, the water lilies, pondweeds, duckweeds, cattails, bulrushes, wild iris, water hyacinth, and rice. Parts of some of these plants extend into the air, but even under these conditions the surrounding air is relatively moist because of evaporation from the water surface. Hence transpiration is not rapid. It is an interesting fact that rice is the only major crop that is a hydrophyte.





Hydrophytes. (*Top*) Mangroves in Jamaica. (Courtesy, M. S. Markle.) (*Bottom*) Waterlily.



Desert near Tucson, Arizona.

Xerophytes. Plants that can grow under conditions in which transpiration tends strongly to exceed absorption are called xerophytes (*xeros*, dry). This condition is called a *low water balance*, for such plants as can live in xeric places must be able to resist, or in some way endure, the tendency to "spend" their water faster than they can acquire it. The low water balance finds its extreme expression in deserts. Here, such plants as cacti, century plants, and other fleshy or succulent species may be said to "hoard" their water. Transpiration is very slow from their water-filled tissues that are richly colloidal and have only small intercellular spaces. For these reasons there is a strong tendency to retain the small amount of water absorbed. But the very conditions that decrease transpiration also restrict the entrance of carbon dioxide, thereby reducing the rate at which photosynthesis can take place. Partly as a result, desert succulents grow extremely slowly.

In contrast with the succulent plants, those species that do not take on a fleshy form (and a majority of desert plants do not) are very profligate with water. Often they have extensive roots and small tops. If the relative areas exposed to the air are taken into consideration, their transpiration rates are much more rapid than are those of mesophytes, when the two kinds are growing in moist soil under identical conditions. When soil water is greatly reduced, however, the xerophyte transpires considerably less than other plants. When the water balance becomes too low the xerophyte ceases to grow, temporarily, while other plants are likely to die. *Xerophytism*, then, seems to be *a condition of the protoplasm that permits a considerable amount of drying without death.* Certain of the xerophytes such as crustose lichens, xeric ferns, certain species of *Selaginella*, black moss and many desert shrubs can remain air-dry for long periods of time without loss of life.

The characteristics of deserts are brilliant sunshine, few clouds, dry air, high temperature, and frequent winds, which jointly greatly increase evaporation. The fact that there is comparatively little moisture in the soil adds much to the difficulty of plants in maintaining a water balance. For this reason, none but xerophytes can live under such conditions.

Giant cactus in flower after an almost rainless year. The photographer stood on top of a high step ladder to take this picture. Tucson, Arizona.

One need not, however, go to a desert to find xerophytes. Cliffs, bluffs, and other excessively drained areas dry quickly, especially if they are exposed to sun and wind, and any plants that are present have little moisture available for absorption. Therefore, no seedlings except those of xeric character are able to survive. Usually these are of the

Irrigation in arid West by which xeric land is changed into productive soil capable of growing mesic crops. (*Top*) Soaking the dry soil. (*Bottom*) Orchard on irrigated area contrasted with brushy scrub where water does not reach. Dry, rocky ledge in right foreground; highway far below; large irrigation ditch wandering through left half of photograph. Water is applied to orchard through small ditches only as occasion demands. (Courtesy, Soil Conservation Service, U.S.D.A.)

more weedy species, such as some of the mustards, grasses, cinquefoils, goldenrods, and mullein.

Examples of xerophytes that are common in the more arid parts of the United States are cactus, yucca, century plant, sagebrush, creosote bush, Russian thistle, and certain grasses, while xeric crop plants are wheat, millet, pinto beans, sorghums, and certain strains of dwarf maize such as those grown by some Indian tribes in the western United States.

Under certain conditions ample water may be present but be available to plants in only limited amounts. This situation is called *physiologic dryness.* Physiologic dryness is sometimes caused by coldness of the soil during the growing season. Roots commonly absorb water rapidly when they are warm, but the rate decreases greatly with a lowering of the temperature. Soil tends to remain cold in many parts of both the arctic tundras and the areas at and above timberline in high mountains. The only plants that can live in these places are dwarf in stature and many of then grow prostrate against the ground. Examples are willows, saxifrages, grasses, sedges, cinquefoils, Jacob's ladder, smartweeds, bluebells, and gentians. Both of these characteristics give protection from the drying effects of the wind.

Excessive amounts of salts of various kinds in the soil solution is one other common cause of physiologic dryness. Such a condition occurs along sea coasts and around inland lakes and ponds in arid regions. Large amounts of dissolved minerals produce such a high osmotic pressure (see pp. 63–64) that absorption into the roots can take place but feebly. Only a few species have sufficiently high osmotic pressure in their cell sap to absorb any water from these solutions. Others dry up and die. Most of the successful plants in such habitats have fleshy leaves and stems, that is, they are succulents. Examples of this type are glasswort, *Salicornia*, Russian thistle, *Salsola*, saltbush, *Atriplex*, and iodine bush, *Allenrolfea*. Others that are not succulent are some of the sedges and short, hard grasses.

Under either of these conditions of physiologic dryness, transpiration tends to keep up with absorption, and a low water balance results. These plants are xerophytes growing in wet soil.

Mesophytes. These are plants that thrive in intermediate conditions of transpiration and soil moisture (*mesos*, middle). Usually they have well-developed roots and relatively large tops, in this way striking a medium water balance. Most of the cultivated crops and garden vegetables belong to this class. Other excellent examples are trees of moist woods such as beeches, maples, hemlocks, and white pines as well as the ferns, mosses, and other plants which make up the undergrowth in these forests. Such plants can endure neither standing water nor excessive drought, but must have their roots in moist soil and their leaves in humid atmosphere almost constantly, especially during the growing season.

Mesic woods, near Indianapolis, Indiana.

Water Balance and Plant Structure. There is close correlation between the place in which a plant grows and its cellular structure. The diversities of anatomy are most easily seen in the leaves, although by no means limited to them. The leaves that were studied in detail in Chapter 3 were of usual mesic types. Comparison of these with those of xero-

phytes and hydrophytes reveals the fact that each contrasts strongly with the other two, both in external appearance and in minute anatomy. It was taken for granted for many years that the observed differences explain sufficiently the functional distinctions between the hydrophytes, mesophytes and xerophytes. But certain facts to be presented in later paragraphs (pp. 369–371) indicate that these differences are to be interpreted more as responses to environmental stimuli than as causes of the variations in water relations. We shall consider first the observed facts; then, the interpretation.

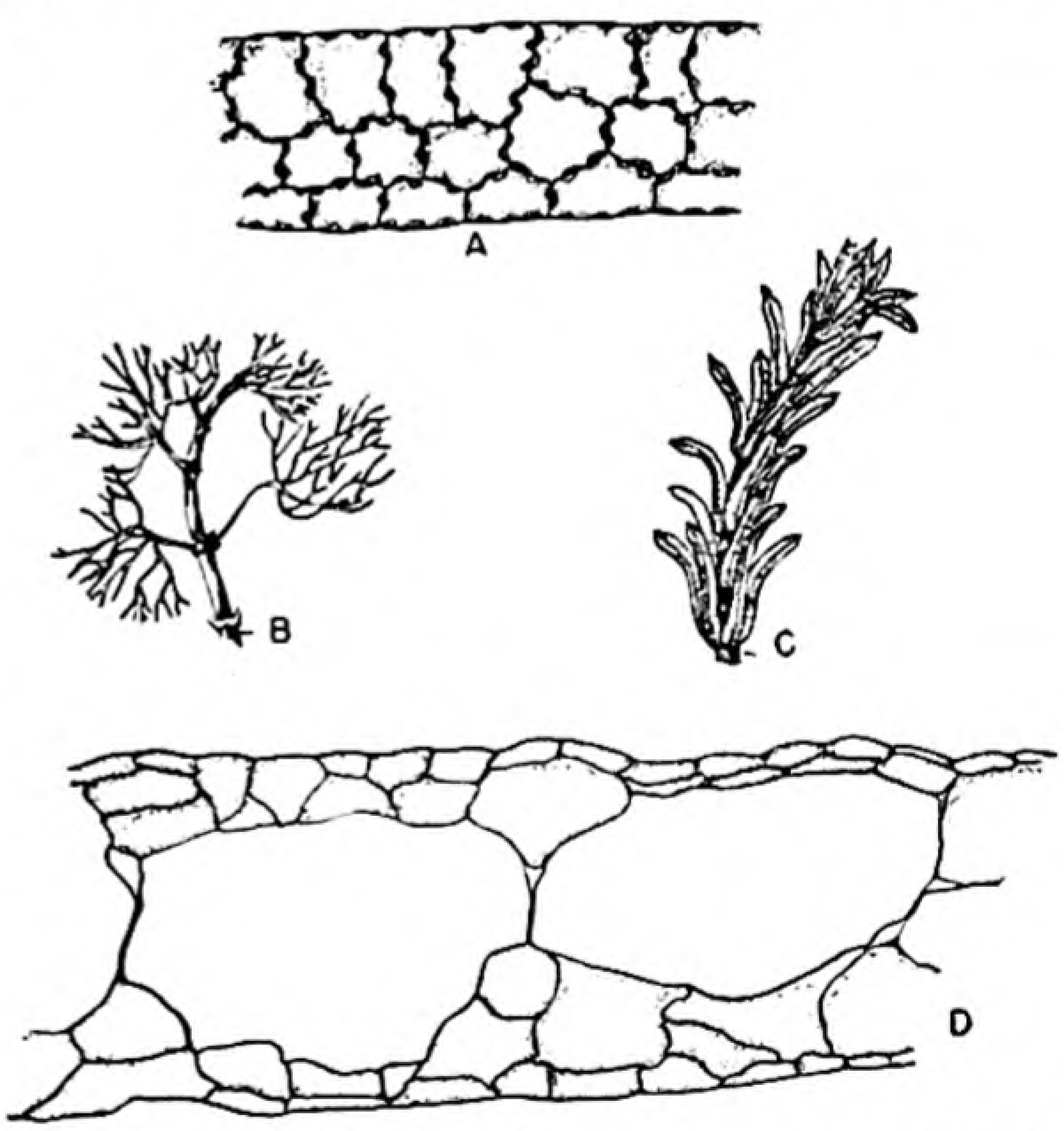
Structure of Hydrophytes. When submerged plants are removed from the water they are usually very thin and limp and dry out quickly. A study of minute anatomy gives the explanation. They dry readily because the cell walls are thin and are extremely permeable to water, for there is no trace of cuticle or other waterproofing coat over their surfaces. They are limp and incapable of bearing their own weight because they have little or no mechanical tissue.

Examination of sections of leaves of these plants by means of the microscope shows them to be of two general types. First, those that are very thin, being only two or three cells thick and having only small intercellular spaces, and second, those having extremely large intercellular spaces surrounded by comparatively few cells.

Submerged hydrophytes do not have functional stomata. Therefore, all such plants normally are completely enclosed by an unbroken layer of epidermis. Within this enclosure there is an intercommunicating system of air spaces extending from the leaves, throughout the stems, and even to all parts of the roots. When photosynthesis is taking place, oxygen, which is the waste product of that process, becomes richly concentrated in the spaces and diffuses into every part of the plant.

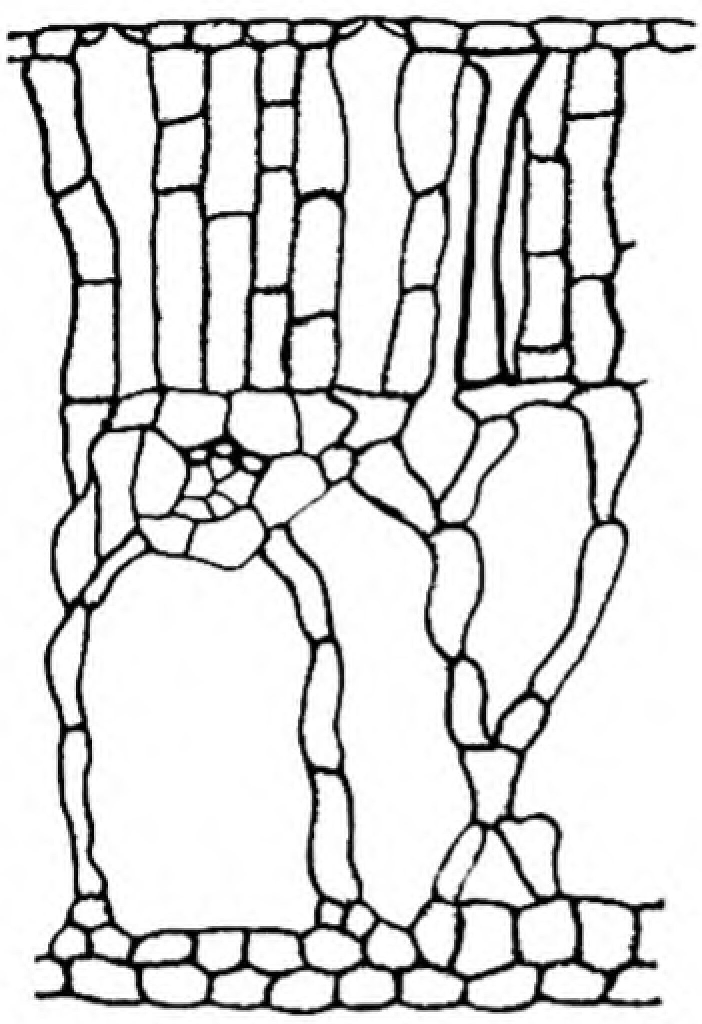
It should be evident from this discussion that submerged leaves, stems, and roots are well adjusted by several characteristics to life under water. The fact that the plants are incapable of producing cuticle or other waterproof coverings is matched by the other fact that transpiration cannot take place under water; the absence of mechanical tissues does not interfere with the support of leaves or other organs of photosynthesis because of the buoying effect of the water; and the extensive internal atmosphere in the intercellular spaces compensates for the relatively low concentration of dissolved oxygen in the water around them. The roots are usually little more than organs of anchorage. They seldom have root hairs and are usually unbranched.

These peculiarities of structure result from combinations of hereditary and environmental effects and can be illustrated by many examples, but only two will be given here. Swamp loosestrife, *Decodon verticillatus*, grows in the form of arching leafy stems that frequently bend over until their tips come in contact with wet soil. There they develop adventitious roots and start new plants. Along swamp margins, instead of touching soil, these tips often grow into open water. Under these conditions the cortex organizes excessive amounts of air tissue below water, greatly increasing the diameter of all submerged parts. The stele remains unchanged.



Structure of hydrophytes. (A) Section of leaf of pondweed (*Potamogeton*) showing very thin leaf and simple structure. (B) Leafy stem of *Myriophyllum* showing finely divided leaves. (C) *Elodea*. (D) Section of leaf of *Valisneria*, showing extreme development of intercellular spaces.

Almost the same principle is shown in the floating leaves of such plants as the water lilies. In these, the part that lies against the water contains large intercellular spaces while that which is in contact with the air has a structure somewhat like that of the leaves of mesophytes, but with all the stomata in the upper epidermis. The long, slender, submerged petioles have extremely large, tubular intercellular spaces extending from the leaf blades to the stems deep in the water.

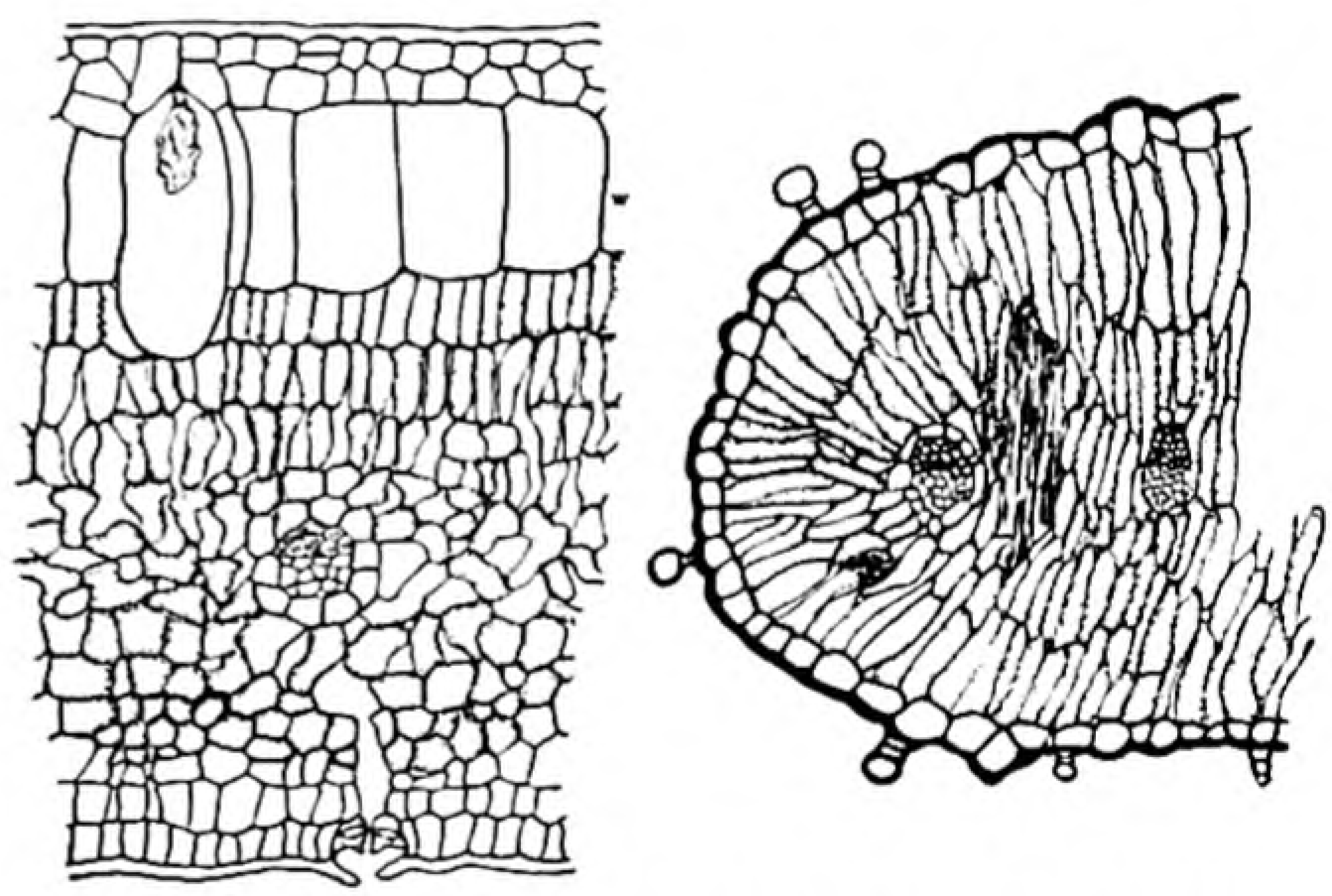


Section of floating water lily leaf showing extreme development of air tissue below water level and somewhat more compact tissues above. Stomata are limited to upper epidermis.

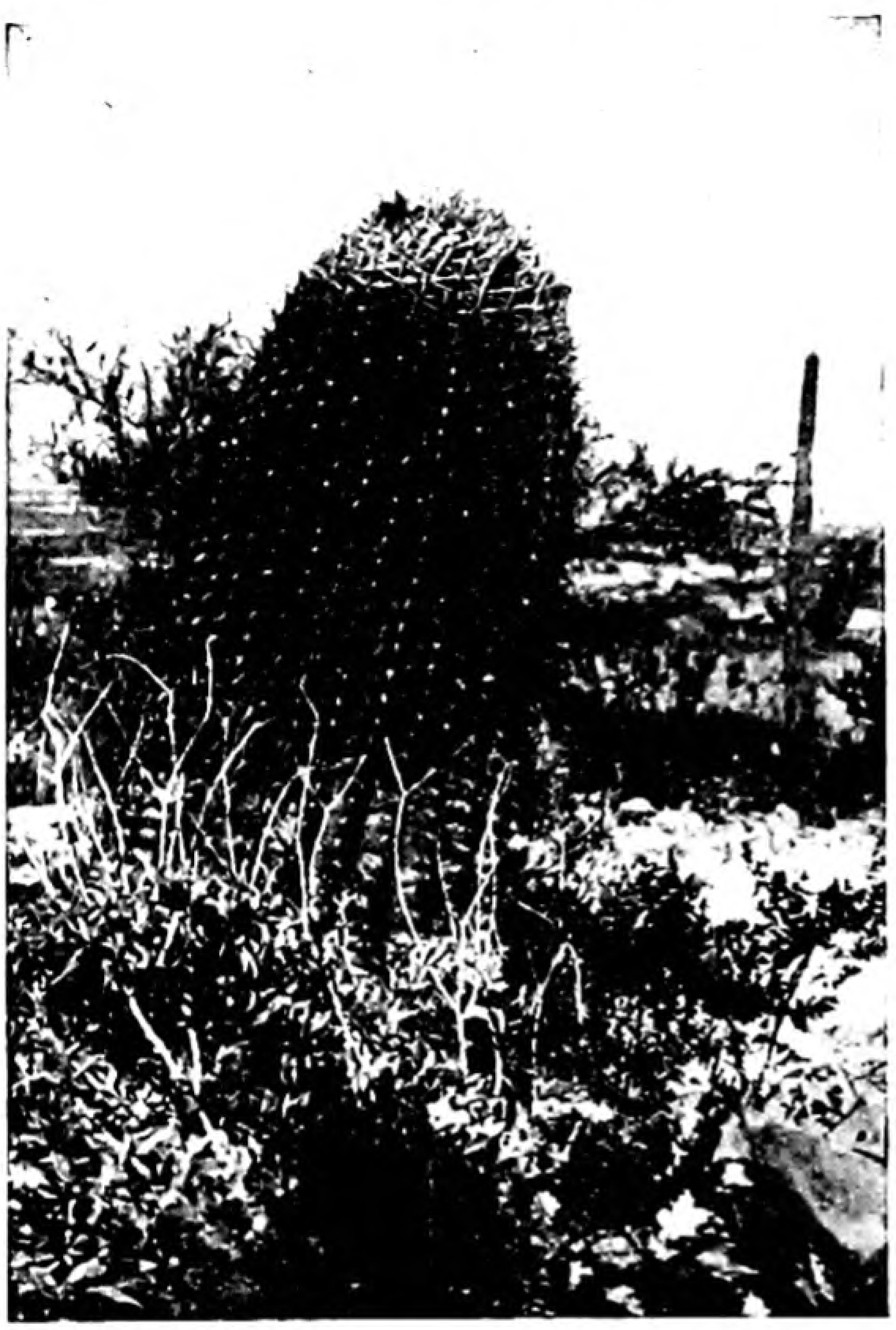
Structure of Xerophytes. The leaves of xerophytes contrast with those of hydrophytes in almost every respect. Commonly the epidermal walls are thick, and in many cases they are covered with a heavy coat of cuticle and sometimes in addition with a layer of wax. Such walls are entirely waterproof. Palisades are usually highly developed, often entirely replacing the sponge tissue, intercellular spaces are comparatively small, and the numerous stomata are sometimes sunken into pits or furrows. In certain species there are large amounts of water storage tissue in leaves, stems, and roots.

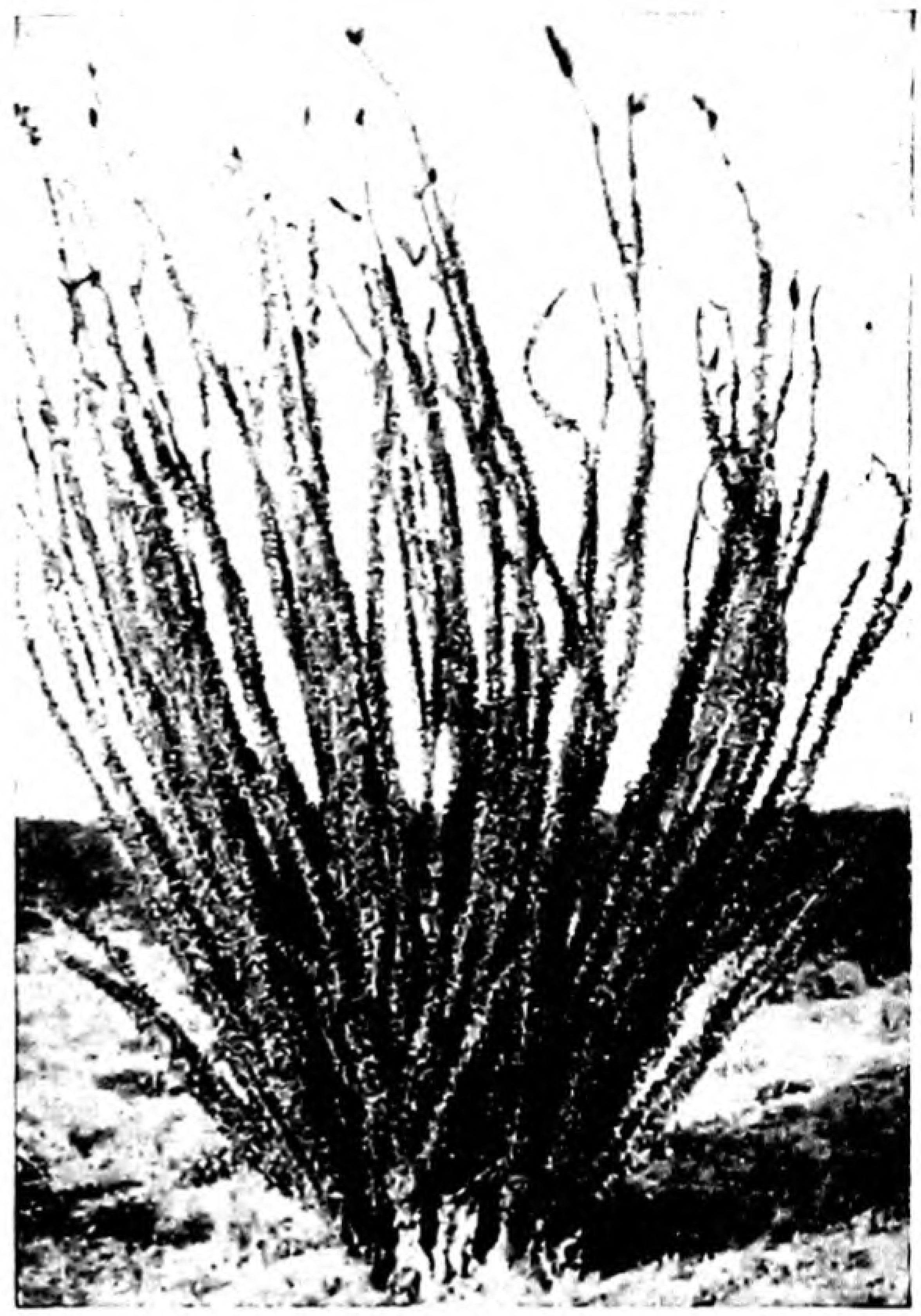
Some xerophytes of the deserts have still more extreme structures by which absorption and transpiration are balanced. Many of the cacti contain great supplies of reserve water and have no functional leaves, carrying on photosynthesis only in the outer layers of the stem. Such plants with no broadened leaf surfaces have very greatly reduced transpiring areas as well as a thick waterproof epidermal covering. Other xerophytes, such as *Ephedra*, take on a "switch" form in which there is no water-storage tissue but in which there is little or no leaf expanse (see the illustration on p. 283), while still others put out mesophytic types of leaves during moist periods, only to drop them promptly when soil and air become dry. Ocotillo (*Fouquieria splendens*), of the southwestern United States, is an excellent example.

Many grasses, especially those that are xerophytes, have a still different type of adjustment (see the illustrations on pp. 31 and 70). The leaves have rows of thin-walled cells in the upper epidermis. At the time of excessive transpiration these cells lose water, thus becoming smaller, by this means folding the leaf so that it closes like a book. In some grasses there are several rows of these specialized cells, causing the leaf to roll when transpiration becomes excessive. The stomata are either all or in large majority in the upper epidermis.



Structures of xeric leaves. (*Left*) *Ficus elastica*, the India rubber tree. Note the highly developed cuticle, the multiple upper epidermis, the inner layer of which is water tissue (w). One cell is forming a limy concretion called a cystolith. The lower epidermis is also made up of three layers of cells and the stoma is somewhat sunken. (*Right*) *Abronia*, a sand verbena. Note the thick outer walls of the epidermis with scattered glandular hairs; the mesophyll made entirely of palisades; and a mass of needlelike crystals.





Types of xeric plants. (*Left*) Barrel cactus, a leafless desert plant with great amounts of water tissue. (*Right*) Ocotillo, a desert switch plant in full leaf. It has leaves when there is ample moisture, and drops them as soon as drought begins. Both photographs taken near Tucson, Arizona.

Such rolling and folding action places the stomata in a protected position; this presumably reduces transpiration. Recent studies have shown that the walls of dry dead leaves long stored in an herbarium are so constructed that they will bring about these movements when moistened and dried as readily as living cells.

The contrast of xerophytes with hydrophytes is almost as great in stems and roots as in leaves. Throughout the xerophyte, intercellular spaces are very small; in many, the wood and other mechanical tissues are extremely compact, hard, and strong, and the roots are numerous and much branched.

Structure of Mesophytes. Mesophytes are, in general, intermediate between the hydrophytes and the xerophytes in growth habit and structure. Their leaves usually have a moderate amount of cuticle, well-developed palisades, and a spongy layer with numerous intercellular spaces. The root systems, on the other hand, tend to be more extensive than those of either hydrophytes or xerophytes. This situation can doubtless be explained by the fact that the mesic environment supplies both oxygen and water in more nearly ideal amounts to the parts underground than does any other, permitting them to develop more fully. There appear to be two factors that are responsible for the poor root development of the hydrophytes. One is a hereditary tendency of some of them to have poorly developed roots; the other is the absence of dissolved oxygen in the water, which greatly reduces metabolism in the cells of the roots, thus restraining their growth.

In xeric environments roots are prevented from attaining fullest development by a lack of available water. Nevertheless, plants can not be xerophytes without very efficient absorbing systems. In some species the roots grow deep into the soil, extending down to a fairly constant water supply. In others they are horizontal and very shallow, a position that permits them to absorb water when only the superficial layers of soil are moistened by light rains. Other xerophytes have a combination of both of these types of root.

Summary of Comparisons and Contrasts. The following summary as applied to dicotyledon leaves will give a basis for discussion in succeeding paragraphs:

Leaf Characters	*Hydrophytes*	*Mesophytes*	*Xerophytes*
Gross structure	Thin; often divided.	Moderate thickness; usually broad.	From none to broad and thick.
Epidermis	Thin and permeable; no cuticle.	Moderately thick; walls usually waterproof with cuticle.	Outer walls usually, but not always, thick; cuticle and wax often extreme.
Palisades	None.	One or two layers; well developed.	Usually multiple; sometimes entirely replacing spongy mesophyll.
Intercellular spaces	Extremely large and numerous.	Moderate in palisades; plentiful in sponge.	Very small.
Mechanical tissues	Poor or none.	Well developed.	In succulents slight; in nonsucculents often extreme.
Stomata	None in submerged parts; relatively few in aerial leaves.	Numerous, in both upper and lower epidermis in herbs but commonly limited to lower epidermis in woody plants.	Small; very numerous and often sunken in pits or grooves.

The Meaning of Xerophytism. It is difficult to avoid giving a superficial interpretation to the contrasting characteristics outlined above. As an example, the waterproof coverings of the leaves of many xerophytes are easily explained as mechanisms that prevent transpiration. To a certain extent this is true, for the removal of a large area of epidermis causes the underlying tissue to become dry rather soon. Nevertheless, before having a clear picture of the meaning of xerophytism it must be understood that the vast majority of plants of arid climates transpire very freely whenever the soil about their roots becomes moist. Therefore, restricted transpiration is not equivalent to xerophytism. In fact, the converse is often true, for a given area of surface of a xeric plant may lose water vapor several times as rapidly as a corresponding surface of a mesophyte belonging to the same genus, if they are both growing in moist soil under identical conditions of temperature, illumination and relative humidity.

Scores of examples could be given to illustrate the last statement, but a few taken from cultivated crops will be sufficient. For many centuries the American Indians living in the semiarid parts of the United States have been successful in growing crops of corn of remarkably xeric nature. The plants seldom become more than shoulder high to a man even when they are given the best of care. If seed is brought in from the mesic corn belt of the Middle West, it is impossible to raise a crop without irrigation. If, however, both of these strains of corn are grown in moist soil, the xeric type transpires much faster from a given area of leaf surface (that is, has a greater *intensity of transpiration*) than its mesic relative. Likewise, there are certain varieties of wheat that are very xeric when compared with others. Accurate experiments have shown that when these two types are grown side by side in the more arid parts of the wheat belt just east of the Rocky Mountains the strains that produce the highest yields are consistently the ones that transpire most rapidly.

These and many other experiments agree in showing that, with the exception of succulents such as cacti, century plants, and a few other fleshy forms, xeric plants lose water very freely whenever it is available to them. Therefore, waterproof coverings over the epidermis offer only a part of the explanation of xerophytism. Very much more important, apparently, is the ability of the protoplasm of xeric plants to remain alive even when it loses a great deal of moisture. These statements should not be interpreted to mean that water is not neces-

Xeric and mesic corn. (*Top, left*) Xeric corn raised by Navajo Indians. (*Top, right*) A few ears of this corn. (Courtesy, Mrs. Pearl B. Caldwell.) (*Bottom*) Mesic corn growing in corn belt of the Mississippi Valley. (Courtesy, Iowa State College.)

sary in the metabolism of xerophytes, for it is. Instead, plants of the desert remain alive but inactive when they become relatively dry, while mesophytes, under the same conditions, die at once.

Controls Over Transpiration. The epidermis, especially when it is covered by a thick cuticle, plays an important part in reducing transpiration. As long as the stomata are open, water vapor can diffuse out very rapidly but when they are fully closed, as they are sometimes in the dark or when the plant wilts, evaporation from the interior of the plant almost ceases. Therefore, stomatal action constitutes an important control over water loss. When the stomata open again, transpiration often is resumed at an extremely rapid rate. After some hours the loss of water is frequently greatly reduced, even though the stomata remain open. These facts strongly indicate that there are additional controls. These seem to be twofold: (1) Plants are complex colloidal systems, and such colloids readily imbibe water but permit its evaporation only slowly, especially in later stages of drying. It is clear, then, that cell colloids powerfully resist such water losses because of their physical structure. (2) When the plant is living under a low water balance, restraint comes about through the difficulty of absorption from a relatively dry soil. Because water does not enter rapidly it cannot move readily through the xylem vessels, and consequently a powerful resistance to evaporation from the transpiring surfaces is set up. That is to say, the energy required to bring about transpiration is almost matched by the resistance to absorption from the low water supply of the soil, and evaporation is greatly retarded.

The following statements summarize the foregoing discussion of the meaning of xerophytism: Characteristic xeric plants transpire with extreme rapidity as long as there is an ample supply of water. They are able to live when their protoplasm has lost a sufficient amount to cause the death of mesophytes or hydrophytes. They retain water imbibed in the cell colloids and contained in the water tubes with such tenacity as greatly to reduce transpiration when extreme xeric conditions are encountered.

Water is highly important in the life of such plants, and down through the ages natural selection probably has played a great part in developing these finer structures and characteristics which enable xerophytes to conserve waning water supplies and to continue to live when the supply fails. But none of these actions is explained primarily by the anatomic features outlined in the tabular summary given on p. 369. Evidently the gross structural features, which are so often considered to be causes of xerophytism, are to a great extent more probably responses to the environmental conditions under which these plants live. In other words, the anatomic peculiarities seem to be largely effects rather than causes.

LIGHT

General Relationships. Plants are affected by light in several distinct ways. It furnishes the energy by which photosynthesis is carried on, in this way supplying food. In the second place plants make certain tropic responses to light, causing them to assume their characteristic shapes. A third effect seems to be in direct conflict with the first. Although light is essential to growth because of the part it plays in photosynthesis, it also has a marked restraining effect. As an example, studies of the date palm show that it does not grow at all in direct sunshine, only slightly in cloudy weather, and most of all at night. While this tree is somewhat extreme in its behavior, it illustrates a general situation among green plants.

Recent studies of plant hormones (see p. 51) offer an explanation of these surprising reactions. It appears that no growth can occur in plants without auxins; that these substances are produced in the growing tips of shoots that are exposed to the light; and that cells, when they are in the light, become both less permeable and less sensitive to growth hormones than when they are in the dark. In other words, growth substances are produced in the light, but they bring about relatively little enlargement of cells except in the shade.

The effects of light can be demonstrated easily by placing one of two similar plants of almost any kind in the dark and the other in strong light. After they have been allowed to grow for some time the one in the light will be short and stocky

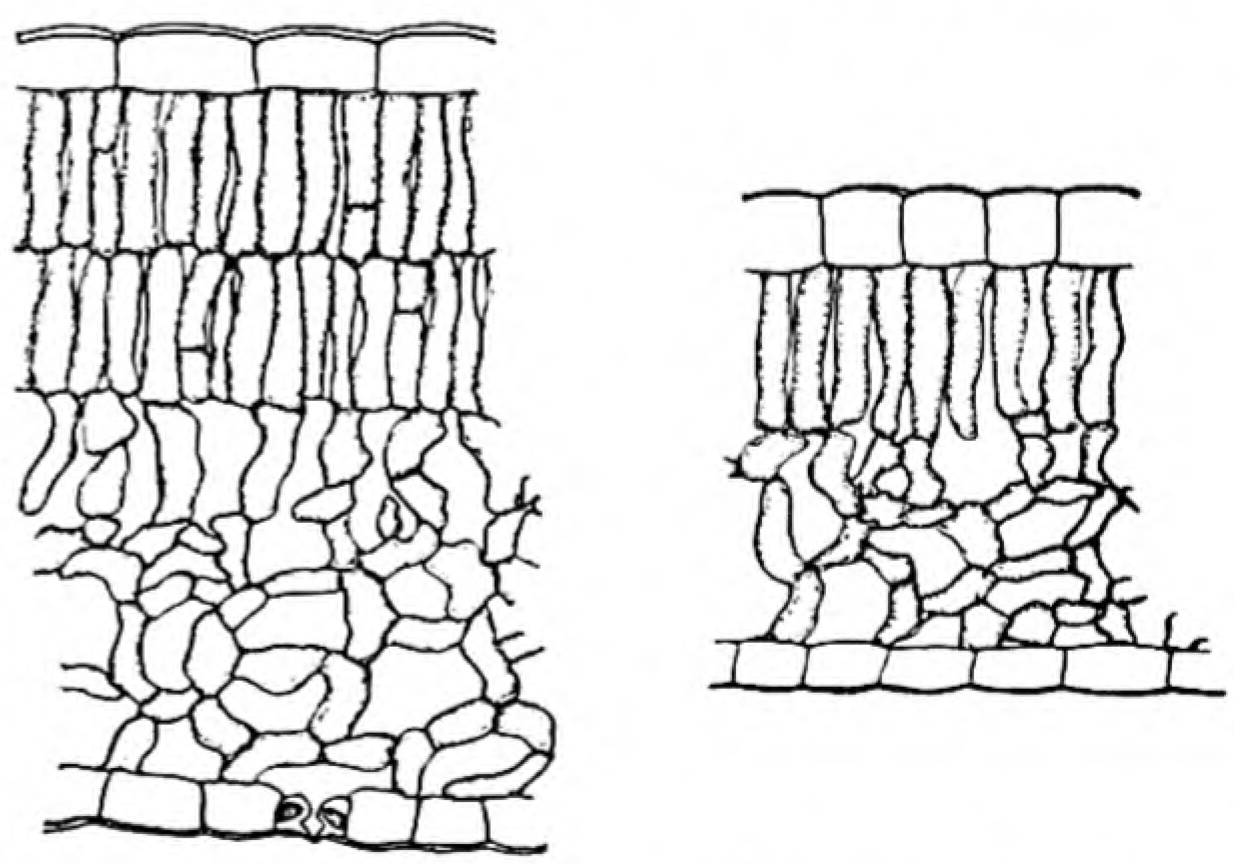
Etiolated bean and potato plants.

as compared with the one in the dark. The latter will be tall and slender with abnormally long internodes.

Plants that are tall and poorly developed because of the lack of light are said to be *etiolated.* They grow in length because of hormones already stored in the seeds or other propagules from which they came, but their development, for some reason, is badly balanced. Such plants, despite their great extension in length, do not reach normal maturity. They do not produce flowers or seeds and are usually unable to reproduce themselves in any way.

Not only is the general shape and degree of development of the shoot dependent upon the amount of light that reaches it, but even the character of the component cells is very much influenced. The cells of leaves are especially responsive to these differences. Structure of sun and shade leaves of some plants varies so much that they may be almost unrecognizable as belonging to the same species. Air leaves, growing in direct sunshine, usually develop a more pronounced palisade tissue and have a more compact spongy mesophyll than those in shade, while the epidermis of such sun leaves often develops thick cell walls and heavy coats of cuticle or wax. Leaves growing under water even in the strongest light do not develop either palisades or cuticle. Those growing in conditions of high transpiration but in the shade do not produce these structures. It appears, therefore, that both palisades and cuticle form in response to the joint action of strong light and high transpiration.

Light Requirement and Light Tolerance. To attain proper growth, some plants require much more light than others; also, some can endure more than others. These differences are expressed in terms of *light requirement* and *light tolerance.* Thus, most of the plants of the prairies have high light requirements; they cannot endure much shade. In



Sun and shade leaves of apple, as seen in sections. (*Left*) Sun leaf. (*Right*) Shade leaf.

contrast with these, most of the mosses that grow on the floor of moist forests quickly die if exposed to the same amount of light that is required by the prairie grasses. These mosses have a low light

requirement and only a slight light tolerance. The following examples illustrate the two types:

Plants with Low Light Requirement	*Plants with High Light Requirement*
Sugar maple	Western yellow pine
Beech	Aspen
Rhododendron	Cottonwood
Fir	Willow
Hemlock	Sumac
Spruce	Silver maple
Linden	Tamarack
Spicebush	Prairie grasses
Bloodroot	Sunflower
Many ferns	Cacti
Many mosses	Creosote bush
Fungi	Mesquite

The requirements and tolerance of light of various species often play important parts in plant distribution. As an example already mentioned, the aspens, which have a high light requirement, often appear in forested regions following heavy cutting or destructive fires. Their leaves may cast sufficient shade to permit the light-intolerant seedlings of maples or pines to establish themselves. These, in turn, eventually grow sufficiently tall to overshadow the light-requiring aspens, causing their death. In this way one association prepares the way for another with less light tolerance and then gives way under the shade of its successor. Such examples can be multiplied many times in the various plant associations. In nursery practice it is customary to grow the seedlings of trees with low light requirements in beds that are somewhat sheltered from the sun by means of lath screens.

There has been some uncertainty whether typical shade plants are more efficient in the processes of photosynthesis than sun plants. Exacting experimentation indicates that chlorophyll is equally effective in all higher plants. The ability of the shade plant to live in greatly reduced light seems to be a capacity to grow little and to remain alive in a half-starved condition. Those plants which require shade are usually damaged by the increased transpiration which results from exposure to direct sunshine and dry air.

Photoperiodicity. Within recent years a considerable number of research workers have found that many plants respond to light in another way. It is a fact of general observation that certain species such as violets, dahlias, cosmos, ragweeds, and asters bloom in the short days either of spring or autumn, while red clover, radish, oats, tomato, lettuce, sweet clover, some species of evening primrose, and hollyhock blossom during the long days of midsummer. It has been found that if these *long-day plants* are left in the light for considerably less than 12 hours of each 24-hour period or if the *short-day plants* are kept in artificially lengthened days by the use of electric lights, neither will produce flowers. On the other hand, maximum vegetative growth occurs under the length of day that prevents flowering in any given species. In other words, plants that flower in short days grow more vigorously in long ones, while long-day plants vegetate more extensively in short ones. Thus, by artificially controlling the length of day, the experimenter can cause a plant to vegetate or to bear seed at will. As an example, radishes can be prevented from producing flowers by placing them in the dark for all but seven hours of each 24, whereas in full length of midsummer days they usually blossom. With the shortened day they continue to produce leaves and to enlarge the fleshy root. On the other hand, if these plants are grown in the greenhouse in winter and the periods of light are artificially lengthened by means of electric lights during a part of the night, they produce flowers and seeds.

A third type is the *indifferent* or *everbearing plant* that produces flowers under conditions good for growth without regard to the length of the period of illumination. Those wildflowers and cultivated plants that begin to blossom in early summer and continue until frost are of this type. Common examples are the everblooming roses and everbearing strawberries.

The underlying causes of the differences between long-day, short-day, and indifferent plants are as yet only partly known, but some evidence is accumulating that hormones probably play a leading part in these controls. Explanations must wait until additional facts can be discovered by investigators.

In nature, short-day plants are prevented from migrating poleward because the summer day becomes gradually longer with increasing distance from the equator. Plants that cannot produce seed in relatively long days cannot migrate great dis-

tances beyond the tropics. In like manner extreme long-day plants are prevented from producing seed and, therefore, from distributing themselves in the 12-hour day of the tropics.

Not only are the flowers and fruits of plants controlled by length of day, but the lengths of their roots and the sizes of tubers or bulbs are as definitely influenced. This is a new field of study and doubtless many new facts about plant growth will be discovered as these researches continue.

THE SOIL

When the earth was newly formed and was very hot there was no soil. Then, if geologists and astronomers are correct, a cool, hard crust of lava and granitelike rock gradually took form, and from these have been derived the beginnings both of soils and of other kinds of rocks.

Down through the ages there gradually appeared great deposits of limestone and other calcium-bearing materials, laid down in water by various means. With the warping of the earth's crust great expanses of these limy strata were lifted above the surface of the water thereby becoming subject to weathering action. The presence or absence of ample supplies of lime in a soil make great differences in its character and productivity.

Soil-forming Forces. Even today, almost every step in the transformations of various kinds of stone and in the organization of soil can be seen still taking place. As an example, a granitic rock or a bed of lava is composed of mixtures of such materials as quartz, feldspar, mica, and often considerable numbers of other minerals.

A very simple, primitive soil forms when weathering causes any rock to disintegrate. Weathering includes several processes. One of these is *solution*, for any kind of rock will dissolve at least to a slight degree whenever it is in contact with water.

Another phase of weathering is *fragmentation*. There are many natural processes that break larger or smaller pieces from any exposed surface of stone. Thus, the outer parts of a rock may absorb a great deal of heat if sunshine strikes it directly. The resulting expansion of the surface while the deeper parts are cool and contracted tends to produce weakened seams. Likewise, when the entire mass has become heated, a shower will cool and contract the surface while the inner part is still expanded. Such repeated shifts in pressures and tensions cause larger or smaller pieces to chip off from the outside and may even produce microscopic cracks extending in various directions through the mass of stone. Water, entering these little fissures, dissolves minute quantities of the minerals, carrying them away where they may be deposited or absorbed by plants. Whenever water freezes in the cracks the expansion of the forming ice opens the cracks still wider and after a time, spaces may become large enough to permit the entrance of small roots. The pressure exerted by their growth still further widens the openings, sometimes even breaking out great masses of rock. The combined effects of all these mechanical and solvent activities reduce solid rock masses to smaller and smaller particles.

Soil forming from granite. (*Left*) Disintegration at an early stage. (*Center*) Soil beginning to organize slightly and a few plants entering. (*Right*) Rock mostly reduced to fine soil particles, largely sand and clay.

Quite as important as either solution or fragmentation is the *chemical transformation* that takes place in many minerals. Quartz (SiO_2) plays little or no part in the chemical reactions within the soil. Instead, it breaks up, becoming sand, and dissolving very slightly. Most of the other rock minerals, on the other hand, besides producing solutions and fragments, undergo chemical changes as well.

The feldspars and related minerals are among the most important of the rock constituents from the standpoint of soil-building. These unite rather readily with water and carbon dioxide, forming clays. The clays vary somewhat, depending on the particular kind of rock from which they have been derived, but all are rich in several of the essential nutrient elements, especially potassium and calcium.

Soil Composition. Clays, together with sand, constitute by far the major part of most soils. Under natural conditions the action of wind and water is continually moving particles from place to place, in this way bringing nutrients together in varying proportions. Nevertheless, such chance combinations are seldom suitable for the maximum growth of plants, although a few probably will live, even though they do not thrive.

Nitrogen compounds are usually all but entirely lacking in these mineral mixtures that are derived from recently disintegrated rocks. The few plants that succeed in growing in such a soil are likely to be poorly developed. Nevertheless, such traces of nitrates as they may absorb are built into their protoplasm and when they die they become the food of microscopic animals and various species of molds and bacteria. These organisms, in the course of their metabolic processes, break down the various organic materials into simpler compounds, many of which can be absorbed and used in the growth of higher plants. In addition, certain of the soil bacteria and blue-green algae fix nitrogen from the air, in this way increasing the total amount in the soil.

Nitrogen-fixing bacteria combine free nitrogen into compounds which become incorporated into their own protoplasm. When they die their complex proteins break down into simpler substances that can be absorbed by the higher plants, thus furnishing them with added nutrients and permitting correspondingly more vigorous growth. With the death of these plants, the compounds containing the elements that are necessary for life and growth are returned to the soil where they may be used again by a succession of others. In this way, unless some living things or their products are removed from a given area, it gradually becomes more fertile.

By activities such as these, a simple, primitive soil that is incapable of supporting more than a meager amount of life, through the centuries gradually becomes more nearly balanced and coordinated into a self-perpetuating source of the various essential mineral nutrients.

The partly decayed bodies of plants and animals are important repositories of the raw materials from which nutrients are gradually set free by the action of microorganisms. This mixture of organic materials constitutes *humus*. Humus is composed largely of fragments of cell walls and protoplasm in various stages of decomposition. The multitude of steps involved in decay is almost beyond comprehension, but through these processes the various nutrients that have entered into the composition of living organisms are gradually released. Therefore, the products of decay that are set free from humus rather closely approach the requirements of the rooted plants.

A well-organized soil is usually composed of a mixture of sand, clay, and humus in various proportions. Such a mixture is commonly called *loam*. There are many kinds of loam, depending on the relative amounts of the various components, as clay loam, sandy loam, etc. These types and the kinds of plants that can grow on them are dependent upon several interacting factors which will be discussed presently.

The texture, appearance, and fertility of the soil vary greatly with its composition. If it is rich in humus it can usually be recognized by a dark brown or black color; if it is sandy it has a grainy or sandy texture; and if it is composed largely of clay it is very compact because it is made up of extremely fine particles. The best farm and garden soils are loams in which these three ingredients are well balanced. Pure sand lacks nutrient salts but, because of the large particles that compose it, permits air and water to circulate freely between the

grains; pure clay is often a rich source of certain of the mineral nutrients, but it becomes very compact, containing insufficient air space for the growth of roots; and pure humus supplies a poorly balanced complex of nutrients, although its organic materials furnish food for myriads of living organisms, including bacteria, molds, and various animals, many of whose activities are indispensable in maintaining satisfactory structure. Although neither sand, clay, nor humus, nor any two of them makes a well balanced soil, when the three occur in mixtures, each contributes its own values while counteracting the disadvantages of the other two.

Another type of soil of outstanding fertility is called *loess.* It is deposited in humid climates as dust carried by wind from distant arid regions. As such, it combines plant nutrients from top soils of widespread origins, giving remarkably well-balanced mineral supplies. Being wind-borne, loess is not stratified as are water deposits, and it can be recognized by its fine-grained amorphous structure.

Loessal deposits often take the form of smooth, rounded hills, but where water erosion occurs, vertical walls tend to remain, in contrast with the sloping sides of ravines in clay or loam.

The Soil Profile. Examination of excavations in many parts of the world reveals a great deal of structure in the soil. Commonly a dark surface layer is present which is very rich in humus. This layer varies from a few inches to a few feet in thickness. Below this layer is a gradual transition to a yellowish stratum of clay. This layer usually is thick and is called *subsoil.* If the cut is sufficiently deep it may reach into the disintegrating parent rock from which the upper layers are being derived. All these layers taken together as a unit are called the *soil profile.*

Soil profiles vary greatly in different parts of the world, depending primarily on three factors: the rock from which the soil has been formed, the climatic conditions that influence its development, and the vegetation growing on it. These three react upon one another to such an extent that they seem to be almost a single unit.

A soil that develops from such stone as granite, in which there is very little calcium, tends to have an acid reaction while that from limestone is almost certain to be neutral or even slightly alkaline. These differences play a considerable part in controlling both the plant and animal life that can thrive in the two localities. As an example, cranberries must have a somewhat acid soil in which to grow and red clover is entirely unable to thrive in that same soil.

Previous discussions have emphasized the fact that climate exerts a powerful control over the kinds of plants that can become established in any given place. Plant associations also greatly influence the soils in which they grow. As an example, the soil profile that develops under an old tall-grass prairie is certain to have a relatively thick top layer that is rich in humus, whatever the original type of soil from which it developed. In contrast, there will be found only a relatively small amount of dark loam in a hardwood forest, because the humus is subjected to changes and disappears relatively quickly through the action of fungi and perhaps of some of the more primitive animals. *The climate controls vegetation and vegetation controls the soil.*

Root Systems and Water Supply. Root systems vary with the different positions of the *water table.* The water table is the level at which the soil is completely filled with water. In their growth directions the roots of many plants, especially of mesophytes, to some degree respond to both moisture and oxygen. This double response causes them to develop in places where there is sufficient water to supply the needs of the plant and enough oxygen to permit respiration in the cells of the roots to take place vigorously. On the other hand, the general form of roots is usually largely controlled by heredity, the responses being only minor deviations from the basic form set by the genes.

Wherever the water table remains above the soil surface, floating plants of various kinds, some with roots and some without, constitute the usual vegetation. Almost all those species that grow attached in soil under water, such as cattails and bulrushes, have shallow, slightly branched roots with large amounts of air tissue.

If the water table is a few feet below the surface, the overlying soil is likely to remain moist through-

out the year and the extensive, finely branched roots characteristic of the mesic forest are best suited to these conditions.

In dry climates, the water level is usually extremely deep and superficial roots are characteristic. Most of the absorption takes place in the upper few inches of the soil when rain or snow falls. The small rootlets that lie just below the surface absorb water with great efficiency as long as the supply lasts. Then the plants usually cease to grow until the next shower.

THE LIVING ENVIRONMENT

The plant has not only a physical environment made up of such factors as water, light, and soil, but also one of living things. The living together of diverse species in a more or less definite relationship is called *symbiosis* (*sym*, with; *bios*, life). A symbiotic relationship may be definite and obligate, such as that of a smut fungus that cannot live except by growing on a corn plant or it may be only incidental like the shading of a fern by a tree. In either instance, however, at least one if not both of the symbionts is affected by the relationship.

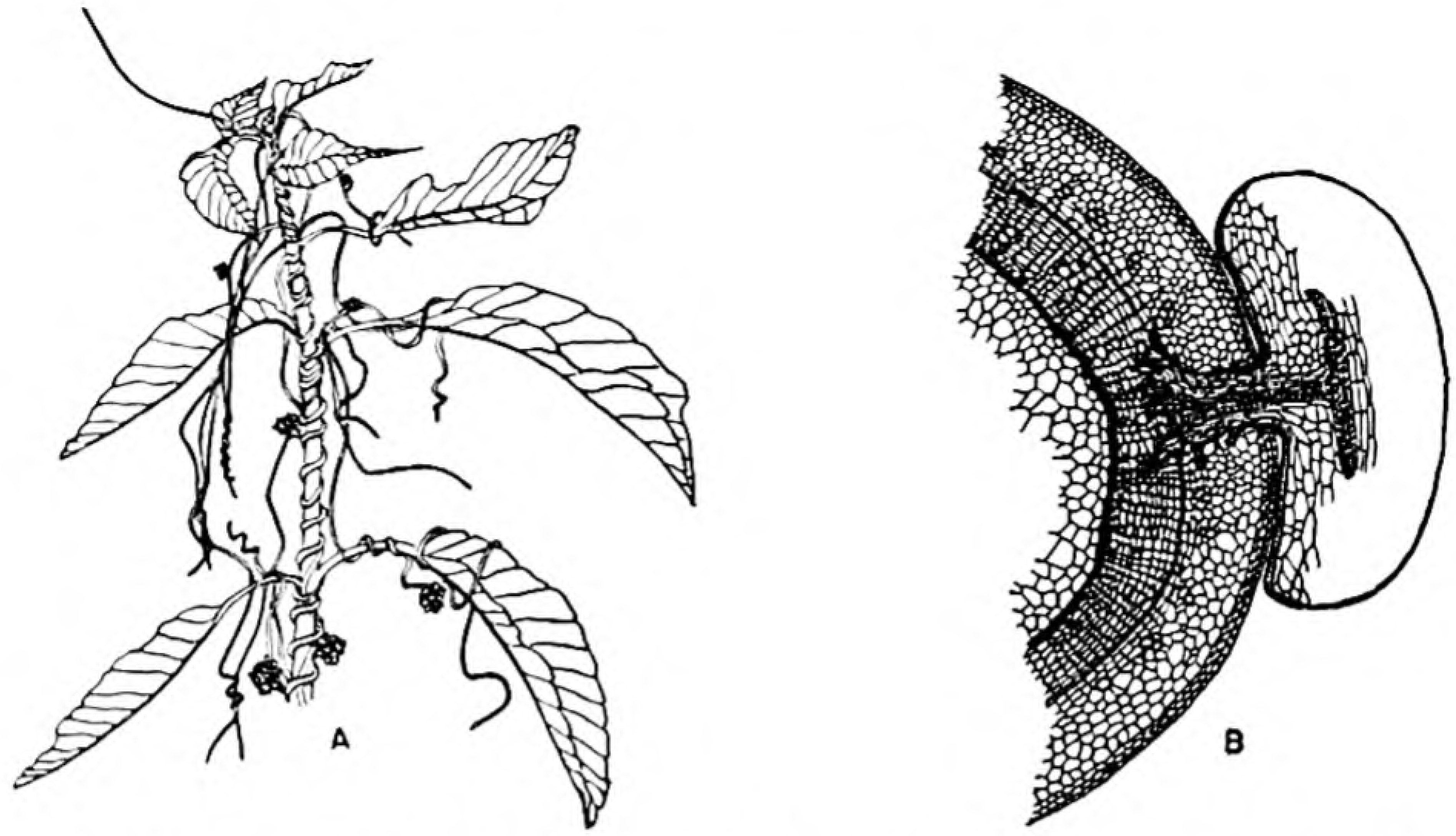
If there is no passage of food between the organisms concerned, the relationship is said to be one of *social symbiosis;* if, on the other hand, either organism derives food directly from the other, it is a *nutritive symbiosis*. Nutritive symbiosis is subdivided into *parasitism*, in which one symbiont takes food from the other, and *mutualism*, in which both parties profit by food exchange, or at least in which neither is harmed.

Social Symbiosis. This relationship may be illustrated by the herbaceous plants that grow in the shade of the trees of a forest. They could not thrive without the protection of the shade, and in turn they somewhat influence the structure of the forest floor by binding the soil particles together and preventing erosion; by retarding the run-off of rain or melting snow, causing the water to soak into the ground; and by forming humus when they decay. Thus each plant affects its neighbors but the influence is purely social and not nutritive. Similarly, *epiphytes* such as Spanish moss and many lichens that live perched on trees (see the illustration on p. 355), and lianas, as for example, grape vines or Virginia creepers growing attached to trees, live in a socially symbiotic relationship with them. In extreme cases, epiphytes become so numerous that they damage the plants on which they grow by shading them. Even the strangling fig eventually kills its host by encircling it with a network of aerial roots. The vast majority of relationships in a plant association are social. While not so striking as nutritive symbiosis, this type is fully as important in the world of living things.

Parasitism. This is a symbiotic relationship in which one individual, the *parasite*, extracts food or other valuable materials from the *host* which is the other party to the association.

Dodder is a parasitic vine closely related to the morning-glories, but instead of depending on its symbiont only for support, it also takes water and

Social symbiosis. The shade and humus produced by forest trees make possible the luxuriant growth of ferns and other undergrowth. Near Lake Michigan.



Dodder. (A) Plant attached to host. Note numerous haustoria penetrating host; also clusters of seed capsules. (B) Section through host and parasite showing xylem of haustorium penetrating to xylem of host and phloem of haustorium extending into phloem of host.

practically all of its food from it. While it is said to have a very small trace of chlorophyll in its cells, probably only negligible photosynthesis occurs. The transfer of materials from host to parasite takes place through short, rootlike projections, called *haustoria*, which penetrate the cortex of the host. Through the haustoria the phloem of the parasite penetrates to that of the host and its xylem extends to the xylem of the host. In this way the parasite has access to both food and water.

The methods of propagation of this plant are interesting. A small amount of food is stored in the seed. The seedling begins its growth in soil and must very soon come in contact with the stem of a suitable host or die of starvation. Once attached to a plant, the roots of the dodder die, and it becomes entirely dependent upon the host for support, food, and water. With ample supplies of these it grows rapid'y, putting out haustoria at frequent intervals and sprawling over all suitable plants which happen to be in its way. In this manner a single individual may reach out and parasitize many of its neighbors if they stand sufficiently close together to be within reach of its spreading branches. Its parasitic tendency is so pronounced that one branch of a dodder plant may insert its haustoria into other branches of itself.

Another parasite that is rather widely distributed, especially in the warmer parts of the United States, is mistletoe. The various species live on trees and shrubs, such as cottonwood, walnut, hackberry, mesquite and numerous conifers. Mistletoe depends on its host for water but its leaves and stems contain a considerable amount of chlorophyll. It is not definitely known whether or not it produces all of its own food, but it seems certain that it must carry on photosynthesis, at least to some extent.

Its method of propagation contrasts with that of dodder. Its drupelike fruits are eaten by birds. The pulp of the fruit is extremely viscid, readily adhering to any object with which it comes in contact. For this reason the seeds often become attached to the beaks or bodies of birds, only to be wiped off on the branches on which they chance to perch. There, the seeds cling and may germinate, inserting their haustoria into the xylem of the tree, establishing new parasites.

Besides the comparatively small numbers of seed plants that are parasites, there are many parasitic fungi and bacteria. Most of the diseases of plants, including trees, shrubs, and cultivated fruits and crops, are caused by parasitic fungi. Plants also parasitize animals. Thus, bacteria are responsible

Mistletoe on ash tree. This photograph was made in late winter and all the leaves belong to the parasite.

for the majority of diseases of both human beings and the lower animals. In turn, numerous animals are parasites on plants. Examples are aphids (often called plant lice), scale insects, and caterpillars.

Mutualism. Mutualism refers to a definite nutritive association of two diverse organisms in such a way as to benefit one or both without harming either. A good example is that of bees gathering pollen and nectar for their own food. They carry away these plant products while at the same time they help in the production of seed by transferring pollen from the anther of one flower to the stigmas of others. Each is definitely benefited by this performance. In a similar way, clover plants profit by the presence of nodule-forming bacteria in the cortex of their roots. Clover acquires valuable nitrogen compounds from the bacteria, while the latter receive such substances as carbohydrates from the clover (see the illustration below).

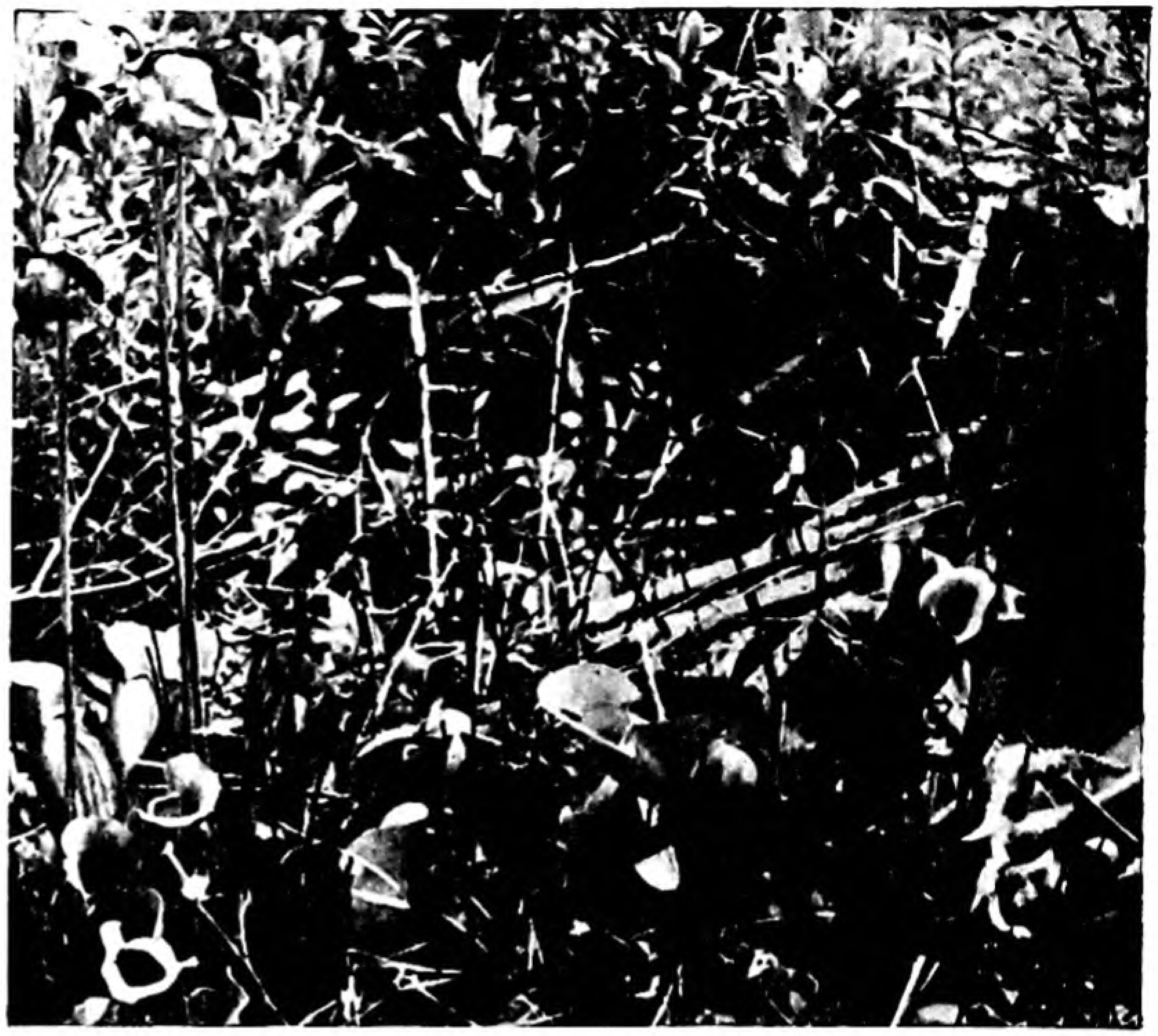
Another mutual relationship that is, as yet, not well understood is that found in *mycorrhizas* (*mykes*, fungus; *rhiza*, root) (see the illustrations on p. 262). These are structures composed of roots and certain soil fungi growing in a symbiotic relationship.

While mycorrhizal fungi are sometimes very important or even essential in the life of certain

Section through nodule on root of wild pea. At very top can be seen the stele. All the part below is the greatly enlarged cortex in which can be seen numerous cells that are dark because more or less completely filled with nitrogen-fixing bacteria.

plants, in other cases they seem to have little or no effect, while in still others they appear to act as mild parasites.

Carnivorous Plants. These peculiar plants exhibit a rare but interesting symbiotic relationship closely allied to parasitism. Three of the best known in North America are sundew and pitcher plants, growing largely in peat bogs and certain other swamplike places, and Venus' flytrap, limited to restricted sandy areas in North and South Carolina. All are green and are capable of carrying on photosynthesis. Their greatest lack seems to be a sufficient supply of nitrogen. In the bogs in which sundew (*Drosera*) and pitcher plant (*Sarracenia*) grow, the peat soil contains only small amounts of nitrates, greatly limiting the supply of one of the elements essential for the production of protoplasm. Besides this handicap, these two plants often have very inadequate root systems and therefore are poorly able to absorb the small amounts of nitrates that are present.


Pitcher plant, showing pitcher-shaped leaves. In peat bog, northern Indiana.

The leaves of the pitcher plant grow in the form of watertight vessels open at the top, or in some species with an umbrellalike lid. In these vessels liquids accumulate. The mouth of the pitcher is very smooth, affording a poor foothold for unwary insects or other little animals which, as a result, often fall into the water. Those that try to climb out find it impossible to do so because of large numbers of coarse hairs that point downward toward the water, causing them to fall back repeatedly until they drown. Their bodies are digested and all but their resistant skeletal remains are absorbed by the plant. Surprising numbers of victims can be found in these pitchers.

The leaves of sundew have bristlelike hairs that secrete viscid drops of liquid in which minute animals, such as insects, stick fast. The struggles of the victim stimulate the marginal bristles to curve inward in such a way as to draw the captive against the leaf surface. Digestive enzymes similar to the pepsin of an animal's stomach are secreted by the leaf. Within a few hours the proteins are digested and absorbed, the hairs have extended again, and the leaf is ready for another victim.

Venus' flytrap (*Dionaea*) (see the illustration on p. 132) obtains its supply of protein in much the same way as sundew, except that the leaf is hinged at the midrib, permitting it to close like a trap. When an insect touches sensitive hairs on its surface the two sides fold together in such a way as to hold the captive. Digestion follows as in sundew.

These three kinds of little plants contribute the only basis for the gruesome stories so often repeated of plants that attract and destroy animals of considerable size, even including man. While carnivorous plants are extremely interesting because of their animallike methods of getting food, they are comparatively rare and of little significance except as examples of the great ability of certain living things to evolve in such a way that they

are adjusted to unusual and hard conditions of life, filling a biotic niche few species can enter.

THE WEB OF LIFE

Thus far these studies have included only interacting pairs or small groups of species. Every species and individual, however, reacts with all others in its vicinity in either a social or a nutritive way, thus establishing a chain, or rather a network, of closely integrated relationships. The definiteness and inclusiveness of these relationships do not become noticeable until some unusual occurrence takes place. As an example, the chestnut bark disease has killed practically all of the chestnut trees over wide areas in the eastern United States. As a result of the death of the trees the flora in those places is changing to a marked degree. Numerous shade-requiring species have died and sun-requiring forms are entering. In this way a fungus disease, by killing one species of tree, is making radical alterations in the whole population. Even a different group of bacteria, fungi, mosses, ferns, wild flowers, insects, and birds are now present solely because a certain fungus was unusually successful a few years ago. Eventually a secondary succession will occur in which some other species will fill the ecological niche left vacant by the death of the chestnuts, and an association that is similar to, but not identical with, the original one, will result. A quotation from "The Orgin of Species," one of the classics of biology, will still further emphasize the interdependence of all parts of the web of life:

"From experiments that I have lately tried, I have found that the visits of bees are necessary for the fertilization of some kinds of clover; but humble-bees alone visit the red clover (*Trifolium pratense*), as other bees cannot reach the nectar. . . . The number of humble-bees in any district depends in a great degree on the number of field-mice, which destroy their combs and nests; and Mr. H. Newman, who has long attended to the habits of humble-bees, believes that more than two-thirds of them are thus destroyed all over England. Now the number of mice is largely dependent, as everyone knows, on the number of cats; and Mr. Newman says, 'Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.' Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district."—CHARLES DARWIN.

Man's Relationship to the Web of Life. Man's activities, especially those of civilized man, too often disrupt the web of life, causing a varied chain of circumstances, many of which are unsatisfactory even in human affairs. Forests that covered half the present area of the United States at the time of the early settlers have been reduced by the axe and the reckless use of fire until only about one-fourth of our area is now forested, and the American Tree Association reports that we are at the present time cutting timber more than four times as rapidly as it is growing. In addition to the resulting loss of products wherever the forest has been removed, the water table in the soil has been lowered; the stage in the succession has, therefore, tended to retreat to a more xeric type, and wells have begun to be less dependable. Other unsatisfactory results come from the fact that, by excessive deforestation and by the destruction of other vegetational cover, flood control is becoming increasingly difficult; soil is washing into the oceans more rapidly than before, thus reducing the fertility of the land; and many species of plants and animals belonging to both forests and grasslands are becoming almost extinct. All these conditions, and others that might be added, are highly unsatisfactory to man himself as well as for the world of living things in general.

Plants as Soil Cover. Where nature is undisturbed, plants usually slowly but gradually improve the soil. The most important means of improvement come from the production of humus. Humus has several valuable functions. Besides providing a continuous supply of necessary nutrients it affects soil texture which in turn controls to a very great extent the supplies of water and air to the roots. Humus, mixed with the mineral parts of the soil, causes the finer particles to flocculate, or in other words, to take on a crumbly consistency that readily admits air into the spaces between the parti-

cles. This structural characteristic is very valuable for plants, makes the soil easy to cultivate and provides an ideal condition for the growth of crops.

In addition, both humus and flocculated soils act as sponges that readily take up water and, because of their colloidal characters, retard the loss, restrict runoff, and reduce erosion. Since humus is a reservoir of nutrients, of oxygen that is used by the roots in respiration, and of water and, since under most conditions it accumulates relatively slowly, it must be maintained with great care if our soils are to continue to be productive. It is always limited to the upper layers of soil and these are the very layers that are lost first when erosion takes place. Since erosion carries away the most valuable soils and with them the best guarantees of continued supplies of food and lumber, the problem of soil conservation is one of world-wide importance and is becoming increasingly a matter of universal concern.

Moist forests, which are the natural plant cover of the more humid parts of the earth, produce fine top dressings of humus. Even heavy rains are quickly taken into the spongy surface only to trickle out relatively slowly into the streams. Much of the rainfall has time to sink deep where the water may remain over long periods of time. Such stored water constitutes a supply that is available in times of drought. Throughout the soil the myriad roots and rootlets of the forest add their actions to bind the particles together and prevent erosion. The total action of the forest, then, restricts runoff, and therefore makes floods less destructive while reducing erosion to a minimum. Experts generally agree that the frequent ruinous floods from the various rivers of the United States are, in part, a result of the excessive cutting of forests that has been taking place since the early European settlers came to this continent. If this conclusion is correct, the cure can be effected in part by the rapid restoration of the forests in the more strategic headwaters of our river systems. Not only will floods be less severe but the flow of rivers will vary less between wet and dry seasons because of water storage in the soil.

The sooner reforestation occurs in the headwaters of streams, the less humus will be wasted and the easier it will be to establish the new forests. In some places it will be necessary only to remove the heavy hand of man, and natural processes will quickly cover the area with plants, but in others, erosion has already gone so far as to make very difficult or even impossible the prompt restoration of forests. This is true especially wherever the soil has washed down to underlying layers of rock.

When the early settlers pushed beyond the forests in their westward migrations, they discovered even greater areas covered with grass. The tall-grass prairies occupied the more humid eastern stretches just beyond the forests, and the short-grass plains continued on into the semiarid West. Under the tall grasses there were deep layers of dark topsoil, made rich by the accumulations of humus down through the ages, while farther west these layers were not so deep nor so dark. In dry climates the amount of humus is restricted both because there is less vegetation to decay and because moisture is not sufficient to encourage rapid disintegration. Nevertheless, over long periods of time considerable amounts have formed even in the dry plains, giving the soil a good quality.

Rains and melting snows soak readily into the soil held by sod-forming grasses, and even when rainfall is too rapid to permit the water to enter as fast as it falls, their close-knit roots and rhizomes prevent excessive erosion and the above-ground parts retard the rate of runoff. Here again plants protect human interests from the action of floods while saving water in the soil where it is useful to both man and the grasses.

Man and Erosion. The tall-grass prairie has now largely disappeared and in its place is the wide expanse of farm land of the upper Mississippi Valley. Where originally the great bluejoint grasses (*Andropogon*) held sway and wild animals, large and small, were numerous, there are now fenced fields of corn, oats, and wheat, and pasture lands artificially seeded with grasses and clovers that yield large amounts of fresh feed and hay for domestic animals. Erosion occurs, but wherever farms are carefully managed it is fairly well controlled. Unfortunately, however, over wide areas almost every shower carries away a small part of the precious

Grasses stopping erosion at a place where the sod has been destroyed a few years earlier.

topsoil and impoverishes the land to some extent. The plow and the cultivator keep the surface loosened and ready to move whenever running water flows over it. In this way the best is gradually slipping away. Even at the rate of a small fraction of an inch per year, it is disappearing much more rapidly than new, mature soil is forming. It is as if a man with a large bank account uses and squanders a little more each year than he deposits. In time he must become bankrupt.

In the semiarid parts of the United States the short-grass sods originally held and slowly enriched the land while successfully supporting large numbers of wild animals. The torrents of rain, characteristic of the region, that occasionally broke through the turf and began to erode away the soil, did only temporary damage because usually the vegetation began to heal the scars before they became extensive.

Into this scene of comparative balance between plants, animals, and soil came the herdsman with his rapidly increasing numbers of cattle, sheep, and

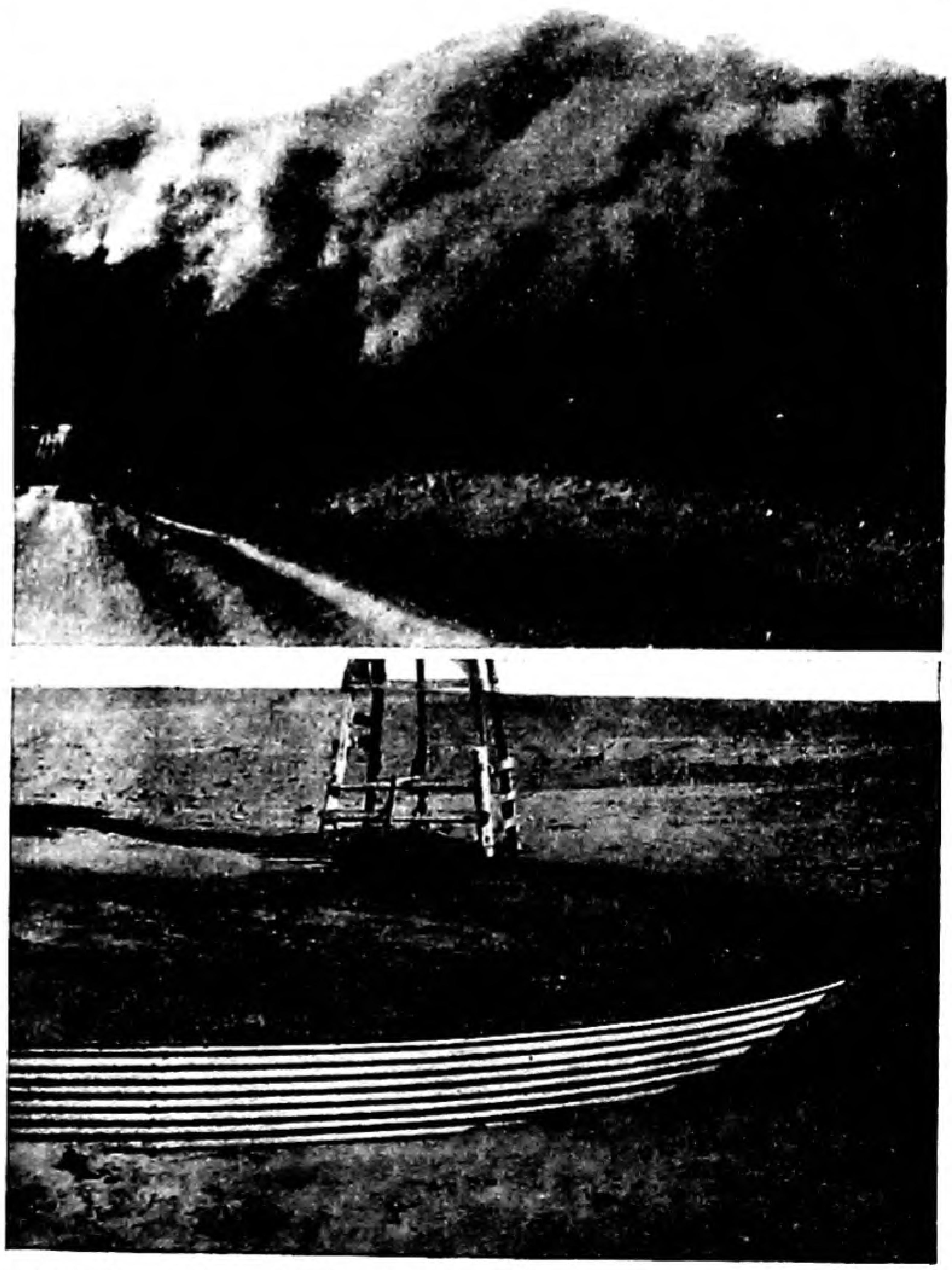
Grasses being replaced by prickly pear cactus because of overgrazing. This cactus cannot be eaten by livestock. Therefore, it sometimes greatly increases when the grass is weakened or destroyed.

horses. Under human protection the numbers of domestic animals soon exceeded by far the number of wild animals they were replacing. As a result, the grass cover gradually weakened.

When man cuts a forest, or when it burns, the destruction is spectacular in the extreme. The entire landscape takes on a new aspect. The green trees are quickly replaced by blackened stumps and snags. Soon erosion sets in still further to alter the landscape. All these changes are dramatic. But when cow hands bring their herds into the short-grass country, the grass, which is only a few inches tall, is eaten down close to the ground. If such pasturage is carried to the extreme, the grass is gradually weakened, and after a period of years unpalatable weeds begin to appear, thin layers of soil wash or blow away, and slow death to the range land sets in. All this takes place so unobtrusively that the damage is not readily recognized. Tramping hoofs have packed the surface until the rains do not soak in as readily as they once did, and the ground therefore remains drier than under conditions of undisturbed nature. Cropping off the tops of the grasses by the grazing animals prevents them from reseeding themselves, and their roots and rhizomes are gradually starved because of the excessive loss of leaves. After a period of years the weakened sod can no longer maintain itself and the topsoil disappears with its priceless humus.

But the herding of domestic animals has not been the only means of destroying the plant cover in the range lands, for many years ago when farmers from the humid eastern and central United States migrated into the semiarid West and Southwest they carried with them the seeds of such crops as corn, oats, and red clover. If they had only understood that mesic plants could not be grown successfully in a semiarid climate many a tragedy might have been averted. It was only in the rainiest years that crops succeeded. At other times near famine occurred.

Even at the present time, although the people of these regions have learned what grains and fruits will grow successfully, great areas of virgin short-grass sod are still plowed under, destroying the native cover in one season, when high prices for cultivated grains overcome good judgment. When low prices or drought make such farming unprofitable, the land is left fallow, producing neither human food nor pasture. Instead, destitution follows.



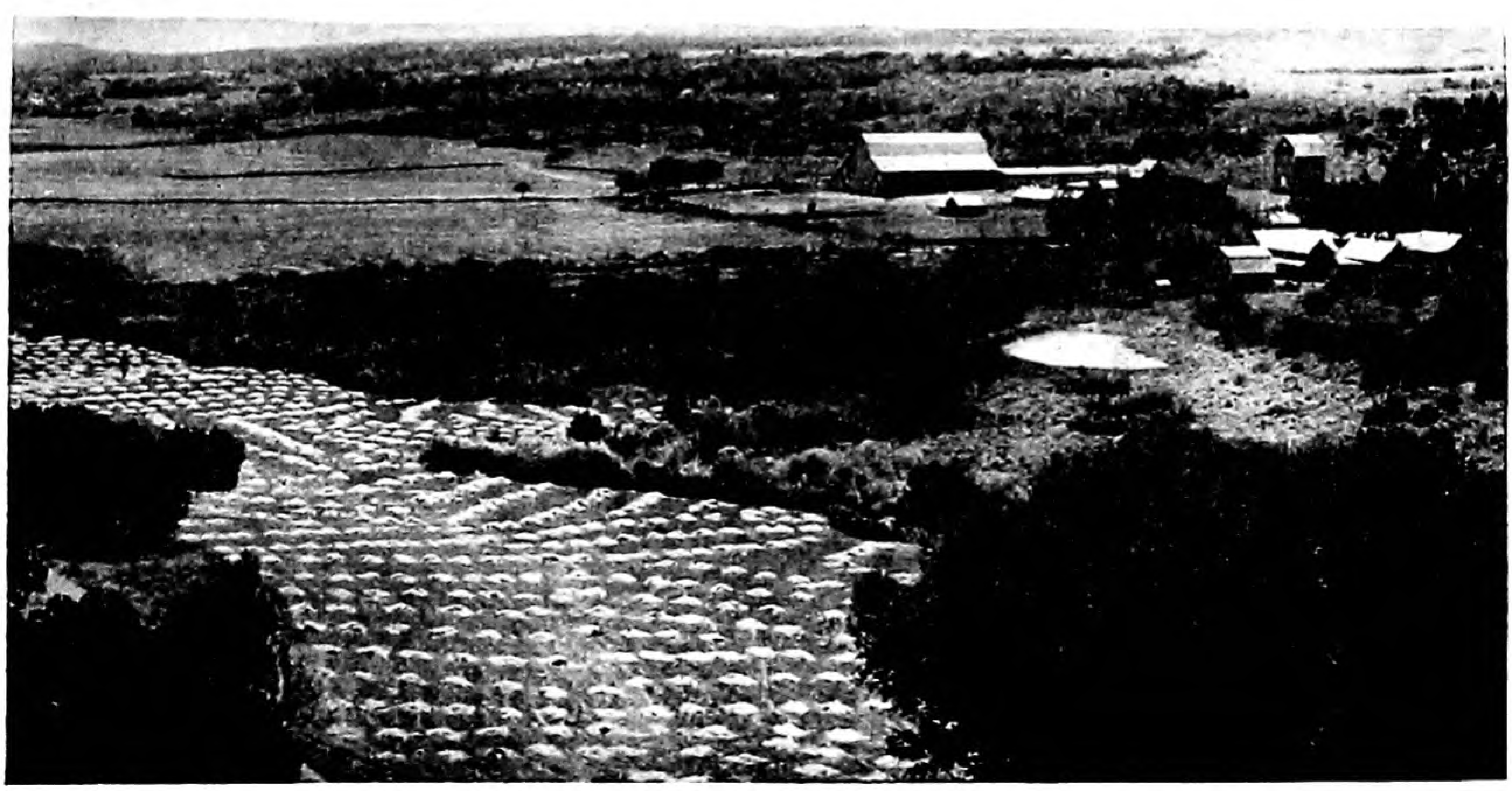
Wind erosion. (*Top*) An approaching dust storm. (*Bottom*) Desolation following dust storm. Neither water nor vegetation remains.

By the axe, by the excessive use of the plow, and by his herds and flocks, man has within a few generations lost for himself, over most of the area of the United States, the best of the soil resources that have been in progress of development for countless centuries. In every section of the country he has been guilty, although usually failing to recognize his fault.

Abandoned, terribly eroded farms over great sections of the East and South; soil laid bare, in places even to bed rock where forests once stood; and the unbelievable dust storms in the West, with domestic animals starving to death or dying for want of water which is completely out of reach—all of these are different symptoms of the same malady: our loss of plants and then of soil.

The Remedy for Erosion. This loss can be regained and the malady remedied in only one way. That way is to replace the plant cover wherever other methods of controlling the soil cannot be found. In places, these perennial covers are slowly being reëstablished, sometimes at great expense. Wise management now can eventually regain for ourselves and for future generations much of the lost value. But wise management depends on the extensive knowledge of trained experts, and wholehearted coöperation on the part of others. For everyone, expert or coöperator, must realize that before man can reach a solution of this world-wide problem, he must realize his almost helpless dependence upon plants.

Aimless Destruction. Most of the mistakes just discussed came as a result of a desperate effort to feed, clothe and house a rapidly increasing population. It may be possible to become sufficiently intelligent and in the future to develop enough social consciousness to undo some of the damage that has been done. In one respect however, we as a people are sadly and inexcusably at fault, and that is in the careless destruction of wildflowers. In several states the wholesale uprooting of native plant life has been so extensive that it has become necessary to pass laws and set up enforcement measures to prevent complete extermination of long lists of plant species. Armloads of wilted flowers discarded along the highways are not uncommon sights in many parts of this country. Too often the picking of these not only removes them



Abundance. Photograph by Merton W. Jones. Barton Ranch, Verdure, Utah.

from the landscape but damages or even kills the plants on which they grow. By such thoughtless actions beautiful displays of orchids, gentians, lotus, water lilies, and ferns, to mention only a few, have been reduced to waste places within the memory of persons yet comparatively young. In some of the eastern states the much-prized trailing arbutus has almost disappeared and parts of the Southwest are being robbed of cacti by merchants who carry away these slow-propagating plants in truck loads. These picturesque species may become rare even in their native homes unless they are protected more carefully in the future. The list might be extended almost indefinitely.

It is not the professional botanist who thus destroys vegetation *en masse*. It is usually the person who understands the least of its real values. Some one has said that the vandal is a person who destroys value without recognizing it. From the standpoint of native wildlife, modern civilized man is often a vandal. Just now a few persons are making a determined effort to save relatively small areas under natural conditions, for study and for the use of future generations. If they are successful, their foresight will certainly be appreciated in years yet to come.

Constructive Activities. On the other hand, man can be and often is a constructive rather than a destructive force. It is sometimes wise to change natural conditions or even deliberately to exterminate certain troublesome species, but difficulties come from changes that are made without looking forward to see what the ultimate results of the action will be.

It is the part of wisdom to cut trees under conditions that encourage the forest to continue to perpetuate itself, thus providing products both for immediate needs and for future generations. Likewise, food and other necessities of life depend on fields of wheat, corn, cotton, rice, sugar beets, sugar cane, and numerous other crops. But these must be planted where less desirable wild plants have previously grown. Increasing acquaintance with plants and added knowledge of their ways of living are making possible the substitution of those that are more desirable from the human standpoint, for less useful natural forms. Thus orchards and vineyards are cultivated in many places; wheat, corn, clover, and alfalfa are grown where only prairie grasses once lived; rice is raised in places that were once unused swamps; and many thousands of acres of land are now irrigated that would otherwise be uninhabited desert.

By proper management, forests can be caused to produce better lumber in larger quantities. Unfortunately, common practice in most places falls far short of present knowledge. Invest'gators have estimated that it would be possible to raise four times as much lumber as is now growing if proper care were applied to all of the tree crops in the United States. What has been said of forests is equally true of most other crops. Civilized man has learned to be efficient in some of his endeavors, but continues to be extremely wasteful and destructive in others.

Man is a very effective part of the world of living things and because of his ability to control other organisms his success will depend in part on the intelligence he uses in dealing with them. In other words, man is a part of the web of life, and whether his actions are wise or foolish, he cannot prevent their effects which will, in myriad ways, react on himself. He controls within limits, but in turn he is controlled by his environment.

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Glossary

abscission [L. *abscissus*, cut away] Separation of leaf, fruit, or other structure from a plant, usually by the formation of a specialized layer, the *abscission layer*.

abscission layer A layer of cells which breaks apart from the twig when a leaf or fruit falls off.

absorption [L. *absorbere*, to suck in] Intake, usually by some form of diffusion, of substances from the outside.

accessory bud [L. *accedere*, to approach] Any bud at a node in addition to the usual axillary bud.

achene [Gr. *a-*, not; *chainein*, to gape] A dry, one-seeded fruit in which the ovary wall remains free from the seed coat and does not burst open. See *grain*.

adventitious [L. *adventicus*, an alien] Organs, as roots or buds, arising from such unusual parts of a plant as leaves or pieces of stem.

aeciospore [Gr. *aikia*, injury; *spore*] A spore produced by the aecial stage of a rust.

aecium (*pl. aecia*) [Gr. *aikia*, injury] A cup-shaped structure containing aeciospores of a rust.

aeration [Gr. *aēr*, air] Supplying with air.

aerial [Gr. *aēr*, air] Organs that grow in air rather than in soil or water.

aerobic [Gr. *aēr*, air; *bios*, life] Living or active only in the presence of gaseous oxygen.

aerobic respiration Respiration in which gaseous oxygen is required.

agar-agar [Malay] A jellylike substance obtained from seaweed and used in making culture media for bacteria and other microörganisms.

after-ripening Chemical and physical changes that must take place before certain seeds can germinate.

aggregate fruits [L. *aggregare*, to collect] A fruit which is made up of many distinct carpels of one flower, for example, the blackberry.

alga (pl. *algae*) [L.] A primitive chlorophyll-bearing plant.

allele [Gr. *allēlōn*, of one another] Either of a pair of contrasting hereditary characters or genes.

allelomorph [*allele;* Gr. *morphē*, shape] Allele.

alternation of generations The alternation of sporophyte (or diploid) and gametophyte (or haploid) generations in a life cycle.

amino acids [*ammonia*] "Building blocks" of the proteins.

amino radical NH_2, a derivative of ammonium (NH_3) and a constituent of amino acids.

ammonification Changing other nitrogen compounds into ammonium, NH_3.

ammonifying bacteria Bacteria which release ammonia in the decomposition of organic matter.

amphigastria [Gr. *amphi*, around or on both sides; *gastēr*, stomach) Rudimentary leaves on the under side of a prostrate leafy liverwort.

amphiphloic [Gr. *amphi*, on both sides; *phloos*, bark) The arrangement of the parts of a stele in which phloem lies both within and without the xylem.

amylase [L. *amylum*, starch] An enzyme which digests starch.

anabolic enzyme [Gr. *ana*, up; *bolē*, a stroke] An enzyme which builds more complex compounds from simpler ones.

anaerobic respiration [Gr. *an-*, not; *aēr*, air; *bios*, life] Respiration in the absence of free oxygen. Fermentation.

anaphase [Gr. *ana*, up; *phainein*, to show] The stage in mitosis in which the daughter chromosomes move to opposite poles.

anatomy [Gr. *ana*, up; *temnein*, to cut] The study of structure. In plants this study is called *plant anatomy* or *structural botany*.

angiosperm [Gr. *angeion*, a container; *sperma*, seed] Any plant of the class Angiospermae; the seeds are enclosed in an ovary.

annual [L. *annus*, year] A plant which completes its growth in one year.

annular vessel [L. *annulus*, a ring] A water tube with ringlike thickenings in the walls.

annulus [L. *annulus*, a ring] A ringlike structure, as that around the stipe of a mushroom, a moss capsule, or a fern sporangium.

anther [Gr. *anthos*, flower] The part of a stamen which produces the pollen.

antheridium [Gr. *anthos*, flower; *-idion*, a diminutive ending] A structure in plants in which sperms are produced.

anthocyanins [Gr. *anthos*, flower; *kyanos*, blue] Pigments which dissolve in cell sap of petals etc., producing such colors as red, purple, or blue.

antibiotics [Gr. *anti*, opposed to; *bios*, life] Products of certain fungi which interfere with the life activities of bacteria and other microörganisms.

antipodal nuclei [Gr. *antipous*, with the feet opposite] Nuclei of the female gametophyte of an angiosperm, lying at the end opposite the egg.

apical [L. *apex*, tip] Pertaining to the apex or tip of a root, stem, or other structure; for example, the apical cell, apical meristem, or apical growth.

apical cell A cell at the growing tip of some plant organs which divides mitotically, producing other tissues.

apical dominance The control by apical tissues of branching or other forms of development in somewhat distant parts of the same organ.

apical meristem Formative tissue at the tip of a root or shoot, in which very active cell division takes place.

archegonium (pl. *archegonia*) [Gr. *archaios*, primitive; Gr. *-gonos*, offspring] The multicellular structure of many plants in which the egg is produced.

arm palisade A mesophyll cell with peculiar infolded walls; common in pine leaves. See *palisade*.

ascocarp [Gr. *askos*, bladder; *karpos*, fruit] The fruiting body of an ascomycete, which contains asci.

ascogonium (pl. *ascogonia*) [Gr. *askos*, bladder; *-gonos*, offspring] The part of an ascomycete which produces asci.

Ascomycetae [Gr. *askos*, bladder; *mykēs*, fungus] The ascus-bearing class of fungi.

ascospore [Gr. *askos*, bladder; spore] A spore produced in an ascus.

ascus (pl. *asci*) [Gr. *askos*, bladder] The spore sac of an ascomycete.

asexual reproduction [Gr. *a-*, not; sexual] Reproduction without sexual means.

assimilation [L. *assimilare*, to make like or similar] Constructive metabolism in which nonliving matter becomes protoplasm.

association [L. *socius*, companion] A community of organisms in which one or more species play controlling parts.

autotrophic [Gr. *auto-*, self; *trophos*, feeder] Applied to plants which are capable of synthesizing foods from inorganic substances; as chlorophyll-bearing plants and certain bacteria. See *heterotrophic*.

auxin [Gr. *auxein*, to grow] A growth-promoting substance.

auxospore [Gr. *auxein*, to grow; spore] In diatoms, a naked cell capable of growing into a mature diatom.

awn One of the slender bristles of the heads of various grasses.

axil of leaf [L. *axilla*, armpit] The angle between a leaf and the stem from which it grows.

axillary bud The bud at the axil of a leaf; also referred to as a *lateral bud* because it is attached to the side of the stem.

axis (pl. *axes*) [L., axle] The principal stem of a plant.

bacillus (pl. *bacilli*) [L. *baculum*, a stick] A rod-shaped bacterial cell.

bark The part of a woody stem or root outside the cambium.

Basidiomycetae [*basidium*; Gr. *mykēs*, fungus] The class of fungi with spores produced externally on a basidium.

basidiospore [*basidium*; spore] A spore produced on a basidium.

basidium (pl. *basidia*) [Gr. *basidium*, a small pedestal] The spore-forming cell or cells of a basidiomycete.

Bennettitales [after John *Bennett*, English botanist] A group of ancient gymnosperms, having short, thick, rather tuberous stems and cycadlike leaves.

berry A type of fleshy fruit formed from a single pistil; for example, grape or tomato.

biennial [L. *bi*, two; *annus*, year] A plant that requires two growing seasons to produce seed or fruit.

binomial [L. *bi*, two; *nomen*, name] A species name consisting of two terms; the first, generic (genus) and the second specific (species). The generic name begins with a capital letter.

biochemistry [Gr. *bios*, life] The chemistry of life processes.

biology [Gr. *bios*, life; *logos*, discourse] Life science.

biotic association [Gr. *biōtikos*, pertaining to life] An organized society of plants and animals; *biome*.

biotic pressure Crowding that results from increasing numbers of individuals within a biotic association.

black mold One of the Phycomycetae having black spores.

blade The expanded part of a broad leaf.

boll A capsule of cultivated cotton containing seeds.

botany [Gr. *botanē*, plant, fodder] The science of plant life.

bract [L. *bractea*, a thin plate] A leaflike structure subtending a flower or flower cluster; in dogwood, sometimes showy and mistaken for a petal.

Brownian movement [after the Scottish botanist Robert *Brown*] The rapid vibratory motion of microscopic particles suspended in a liquid or gas.

Bryales [Gr. *bryon*, moss] The order of plants comprising the true mosses.

Bryophyta [Gr. *bryon*, moss; *phyton*, plant] The division of the plant kingdom comprising the mosses and liverworts.

bud An undeveloped branch or flower.

bud scale A specialized protective leaf enclosing the tender parts of a bud.

bulb [L. *bulbus*] A short stem surrounded by fleshy leaf bases which serves as a means of vegetative propagation in some plants, for example, onion and tulip.

bulliform cell [L. *bulla*, a bubble] A peculiar type of enlarged epidermal cell common in grass leaves, causing folding or rolling when the leaf wilts.

bundle sheath A layer of cells which envelops the vascular tissues of a vein in a leaf.

calcium pectate [L. *calx*, lime; Gr. *pēktos*, congealed] The compound formed when pectin unites with calcium, cementing adjacent cell walls firmly together.

callus [L.] A layer of tissue which forms over a wound on a tree trunk.

calorie [L. *calor*, heat] The standard measure of energy. The large calorie is the amount of energy, expressed as heat, required to raise the temperature of one liter of water 1°C.

calyptra [Gr. *kalyptra*, a head cover] The top of the archegonium of a liverwort or moss, which covers the capsule.

calyx [Gr. *kalyx*, cup] A whorl of sepals, usually green or inconspicuous, enclosing other floral parts in the bud.

cambium [L. *cambium*, exchange] A sheet of meristem which produces secondary xylem, phloem, and rays.

capillitium [L. *capillus*, a little hair] In the slime molds, the dried network of cytoplasm which forms the framework of the sporangium, enclosing the spores.

capsule [L. *capsula*, a little box] A spore case of moss or liverwort; the gelatinous outer wall of bacteria; a dry dehiscent fruit, composed of two or more carpels and containing numerous seeds.

carbohydrase [carbohydrate; *-ase*, an enzyme] An enzyme which digests carbohydrates.

carbohydrate [L. *carbo*, coal; Gr. *hydōr*, water] A compound such as sugar, starch, or cellulose, composed of carbon, hydrogen, and oxygen.

carboxyl radical The organic radical —COOH.

carnivorous plant [L. *carnis*, flesh; *vorare*, to devour] A plant which traps and digests animals, especially insects.

carotin [L. *carota*, carrot] An orange-colored compound commonly associated with chlorophyll in the chloroplasts. Chemically, it is a lipochrome, the precursor of vitamin A.

carpel [Gr. *karpos*, a fruit] A simple pistil or one unit of a compound pistil; sometimes considered to be the megasporophyll of a seed plant.

carpogonium [Gr. *karpos*, a fruit; *-gonos*, offspring] The egg-producing structure of a red alga.

caruncle [L. *cars*, flesh] A spongy outgrowth from the testa of certain seeds, for example, castor bean.

caryopsis [Gr. *karyon*, a nut; *opsis*, appearance] The one-seeded fruit of a grass. The ovary wall is united to the seed coat; *grain*. See *achene*.

cast Material deposited in cavities of stone left vacant in a fossil by the disappearance of plant or animal remains.

catabolism [Gr. *kata*, down; *ballein*, to throw] Destructive metabolism.

catalyst [Gr. *kata*, down; *lysis*, a loosening or dissolving] An activator or a retarding substance in a chemical reaction, which does not become a part of the product of the process.

catkin Ament; a tassel-like inflorescence.

cell [L. *cella*, a small room] An organized mass of protoplasm containing a nucleus or nuclear material. In most plants the cell secretes a wall of cellulose or other material around itself.

cell sap The very dilute contents of a vacuole.

cellulase [L. *cellula*, a small room; *-ase*, an enzyme] An enzyme which digests cellulose.

cellulose [L. *cellula*, a small room] A carbohydrate which is the main constituent of most plant-cell walls; a polysaccharide.

Cenozoic Era [Gr. *kainos*, recent; *zōē*, life] The geologic era which follows the Mesozoic Era.

chalaza [Gr. *chalaza*, hail] The attachment of an ovule to the scale in a conifer or to the ovary in an angiosperm.

chemical bond [Arabic *kīmiyā*, infusion] The mechanism by which atoms are held together in a molecule.

chemotaxis [chemical; Gr. *tassein*, to arrange] The response of a motile cell or organism to a chemical stimulus.

chemotropism [chemical; Gr. *tropein*, to turn] A response, by turning or bending, to a chemical element or compound such as oxygen, carbon dioxide, or nitrate.

chlamydospore [Gr. *chlamys*, a mantle; spore] A spore, often with a thick wall, characteristic of certain fungi, especially smuts.

chlorenchyma [Gr. *chlōros*, green; *enchein*, to pour in] Chlorophyll-bearing tissue.

chlorophyll [Gr. *chlōros*, green; *phyllon*, leaf] The green pigment of plants which is essential to photosynthesis.

chloroplast [Gr. *chlōros*, green; *plastos*, formed] A chlorophyll-bearing body.

chromatid [Gr. *chrōma*, color; *-idēs*, descendent] Daughter chromosome; one of the two chromosome halves produced during metaphase in mitosis.

chromatin [Gr. *chrōma*, color] A nuclear substance deeply staining in certain dyes, from which chromosomes are formed and which contains or carries the genes.

chromatophore [Gr. *chrōma*, color; *pherein*, to bear] A color-bearing plastid.

chromoplast [Gr. *chrōma*, color; *plastos*, formed] A color-bearing plastid.

chromosome [Gr. *chrōma*, color; *sōma*, body] A deeply staining rod or thread of chromatin which becomes evident during mitosis and meiosis. The chromosomes contain or carry the genes.

chromosome aberration [L. *aberrare*, to wander away] Deviation from usual chromosome behavior.

Chrysophyta [Gr. *chrysos*, gold; *phyton*, plant] A group of plants, the golden algae, so named because of their rich yellow color caused by large amounts of carotinoids.

cilium (pl. *cilia*) [L., eyelash] A whiplike or hairlike protoplasmic projection from a cell, serving as a locomotor organ.

circinate vernation [Gr. *kirkinos*, a circle] Coiled arrangement of the immature parts of leaves of such plants as ferns.

cleistogamous flower [Gr. *kleistos*, closed; *gamein*, to marry] A flower in which fertilization occurs without opening, for example, certain violets.

climax association [Gr. *climax*, a ladder] A community in which a sere tends to come to an end after a long period of time; an established organization which does not readily give place to another except because of a marked change in environment.

club moss A modern member of the ancient division of plants called *Lycopsida*.

coccus (pl. *cocci*) [Gr. *kokkos*, a grain] A spherical bacterial cell.

coenocyte [Gr. *koinos*, common; *kytos*, cell] An organism in which numerous nuclei are distributed through the cytoplasm.

coleoptile [Gr. *koleos*, sheath; *ptilon*, soft feather] A sheath around the epicotyl of a grass embryo.

coleorhiza [Gr. *koleos*, sheath; *rhiza*, root] The sheath investing the embryonic root of a grass.

collenchyma [Gr. *kolla*, glue; *enchein*, to pour in] A mechanical tissue with greatly thickened cellulose walls at cell corners.

colloidal state [Gr. *kolla*, glue; *eidos*, like] Matter in a fine state of dispersion throughout a continuous phase. Most plant colloids are capable of imbibing water.

columella [L., a little column] The inner framework of the sporangium of bread mold or of the capsule of bryophytes.

columnar The form of an entirely unbranched tree trunk with a crown of leaves at the top, for example, the palm tree.

commensalism [L. *cum*, with; *mensa*, table] Nutritive symbiosis in which both symbionts profit by food exchange or at least in which neither is harmed; *mutualism*.

community A group of organisms living together in a more or less well-organized manner.

companion cell A long cell which is associated with a sieve cell in the phloem, both originating from a common mother cell.

compass plant A plant whose leaves, when growing in strong sunshine, twist on their axes until the blades face east and west with the edges assuming a north-and-south position.

compound [L., *cum*, together; *ponere*, to place] A substance formed by the chemical union of two or more elements in definite proportions.

conceptacle (L. *concipere*, to receive) One of a number of special cavities in the tips of branches of the thallus of certain brown algae, where sporangia or gametes are borne.

conidiophore [Gr. *konis*, dust; *pherein*, to bear] A short branch of fungal mycelium which produces conidia.

conidium (pl. *conidia*) [Gr. *konis*, dust] A type of aerial asexual reproductive cell, usually produced in chains at the tips of conidiophores.

conifer [L. *conus*, cone; *ferre*, to bear] Any member of the order Coniferales.

Coniferales [L. *conus*, cone; *ferre*, to bear] An order of gymnosperms which includes many of the cone-bearing trees, such as the pines, spruces, and firs.

conjugation [L. *cum*, with; *jugare*, to yoke] The fusion of two isogametes.

continuous phase The medium in which are distributed the particles constituting the disperse phase of a colloid.

continuous siphonostele Siphonostele, especially in higher plants, having very narrow xylem rays. See *siphonostele*.

Cordaitales [after the Austrian botanist, A. J. *Corda*] A group of ancient gymnosperms. Tall trees with trunks similar to those of modern conifers. The Cordaitales appear to have descended from the Cycadofilicales.

cork cambium A meristem which produces an outside coating of cork on stems and roots. It usually develops from cells of the cortex.

corm [Gr. *kormos*, a tree trunk] A short, vertical, bulblike underground part of some plants, more or less enveloped by thin, papery leaf bases, for example, crocus, gladiolus, and jack-in-the-pulpit.

corolla [L. diminutive for *corona*, crown] All the petals of a flower taken as a unit.

cortex [L. *cortex*, bark] The tissues of a plant between the epidermis and the stele.

corymb [Gr. *korymbos*, a cluster of flowers] A type of indeterminate inflorescence like a raceme except that the corymb has a very short main axis and the outer pedicels are considerably elongated, in this way producing a convex or flat-topped cluster, as in red haw and some of the cherries.

cosmopolitan species [Gr. *kosmos*, world; *politēs*, citizen] A species of very wide distribution.

cotyledon [Gr. *kotylē*, a cup] A seed leaf.

crustose [L. *crusta*, a crust] Growing as a crust attached to the surface of the substratum. The term usually applies to a form of lichen.

cuticle [L. *cutis*, skin] A fatty or waxy waterproof layer over the surface of the epidermis. See *cutin*.

cutin [L. *cutis*, skin] A mixture of fatty and waxy compounds often found in combination with cellulose in outer cell walls of epidermis which is exposed to the air.

Cyanophyceae [Gr. *kyanos*, dark blue; *phykos*, seaweed] Blue-green algae.

Cycadales [Gr. *kykas*, coco palm] The most primitive order of living gymnosperms.

Cycadofilicales [Gr. *kykas*, coco palm; L. *fili*, fern] The most primitive group of ancient gymnosperms, showing both fernlike and cycadlike features.

cyclosis [Gr. *kyklos*, a circle] The streaming of protoplasm in a cell.

cyme [Gr. *cyma*, a swelling, a cabbage sprout] An inflorescence in which every floral axis and every one of its branches terminates in a flower. A determinate inflorescence.

cystocarp [Gr. *kystis*, bladder; *karpos*, a fruit] The spore-producing part of a red alga.

cytoplasm [Gr. *kytos*, a hollow place; *plasma*, anything formed or molded] The cell aside from the nucleus.

decay [L. *de-*, down; *cadere*, to fall] Decomposition, usually by the action of bacteria and fungi.

deciduous [L. *decidere*, to fall off] Shedding the leaves at the end of the growing season; not evergreen.

dehiscence [L. *dehiscere*, to gape] The bursting open of a fruit, sporangium, etc., along a definite line, thus discharging the contents.

deliquescent branching [L. *deliquescere*, to dissolve] Dividing and subdividing of branches into smaller ramifications.

denitrification Liberation by bacterial action of free nitrogen or ammonium from nitrogenous compounds. In the soil such loss occurs only when there is a marked lack of oxygen, as when the soil is very wet.

determinate inflorescence The type of inflorescence in which the apical meristem of the floral axis organizes into the parts of a flower, thus terminating growth. See *cyme*.

diastase [Gr. *diastasis*, separation] Amylase; any enzyme which digests starch.

diatom [Gr. *diatomos*, cut in two] Unicellular alga belonging to the Chrysophyta.

diatomin [Gr. *diatomos*, cut in two] The brown pigment in diatoms.

dicaryon (pl. *dicarya*) [Gr. *di*, two; *karyon;* nut] A binucleate cell especially common in certain groups of ascomycetes and basidiomycetes.

dichotomous branching [Gr. *dicha*, in two; *tomos*, a cut] Branching by repeated forking of the main axis.

dicotyledon [Gr. *di-*, two; *kotylēdōn*, a cup] An angiosperm whose embryo has two cotyledons.

differentiation [L. *differe*, to carry apart] The process of meristematic or embryonic tissues becoming specialized into the various mature tissues.

diffusion [L. *diffundere*, to pour out] Dispersion of one substance as a solution or gas into another.

digestion [L. *digerere*, to dissolve] Changing insoluble foods into soluble forms by means of enzymes.

dioecious [Gr. *di-*, two; *oikos*, house] Having male reproductive organs in one individual and female in another; separate sexes.

diploid chromosome number [Gr. *diploos*, double; *eidos*, form] Having two sets of chromosomes.

disaccharide [Gr. *di*, two; *sakchari*, sugar] A sugar whose molecule can be hydrolyzed or digested into two monosaccharide ($C_6H_{12}O_6$) molecules, for example, sucrose.

disease [Old French *dis-*, apart; *aise*, ease] Disturbance of normal metabolism, usually by invading bacteria or fungi.

disperse phase [L. *dispergere*, to scatter] The particles in a colloidal system which are distributed throughout the continuous phase of that system.

dissected siphonostele [L. *dissecare*, cut apart] A siphonostele (a stele with central pith) having wide rays between the vascular strands.

dissemination [L. *disseminare*, to sow] Scattering or sowing seeds or spores.

domestication [L. *domus*, house] Taming or cultivating an animal or plant.

dominance [L. *dominus*, master] The overshadowing of a gene by its allele in heredity; the controlling effects of one species in a biotic community.

dominant species [L. *dominus*, master] A controlling species in a biotic association.

dormant bud [L. *dormire*, to sleep] An inactive bud, such as a winter bud, consisting of three parts: protective scales on the outside, undeveloped leaves, and an apical meristem.

dormant seed A vegetatively inactive seed.

dorsiventral plant body [L. *dorsum*, back; *venter*, the belly] A plant having distinct dorsal and ventral surfaces, as the liverworts.

double fertilization In angiosperms, the fertilization of the egg and endosperm nucleus by the two sperm nuclei.

drupe [Gr. *druppa*, an overripe olive] A stone fruit; one in which the endocarp (inner layer of the ovary wall) ripens as a hard coat.

ecology [Gr. *oikos*, house; *logos*, discourse] The branch of biology which deals with the organism in relation to its surroundings.

ectophloic siphonostele [Gr. *ektos*, outside; *phloos*, bark] A stele with central pith and with the phloem outside the xylem.

ectotrophic [Gr. *ektos*, outside; *trophikos*, nourishing] A form of mycorrhiza in which the fungus receives food from the green plant without actually entering its cells.

elater (pronounced ĕl'ater) [Gr. *elatēr*, a driver] An elastic or hygroscopic filament which pushes the spores out of a sporangium.

embryo [Gr. *en*, in; *bryein*, to swell] A young organism; a young sporophyte.

embryo sac The female gametophyte of an angiosperm.

embryonic root The root-forming meristem of a plant embryo.

endemic [Gr. *en*, in; *dēmos*, district] A group of organisms confined to a limited area or region.

endocarp [Gr. *endon*, within; *karpos*, fruit] A specialized inner layer of the pericarp, for example, the stony portion of a drupe.

endodermis [Gr. *endon*, within; *derma*, skin] The innermost layer of cortex of a vascular plant.

endosperm [Gr. *endon*, within; *sperma*, seed] Food in a seed aside from the embryo.

energy [Gr. *en-*, in; *ergon*, work] Capacity to perform work.

endotrophic [Gr. *endon*, within; *trophikos*, nursing] A form of mycorrhiza in which the fungus grows from the soil into living outer cells of the root.

environment [Old French *en*, in; *viron*, circle] Surroundings.

enzyme [Gr. *en*, in; *zymē*, yeast] An organic catalyst produced by a living cell, which accelerates a specific chemical reaction. All physiological processes are probably carried on by numerous enzymes, each bringing about its one single step.

epicotyl [Gr. *epi*, upon or above; *kotylē*, cup] The immature shoot of the embryo of a seed plant, which is attached just above the cotyledon or cotyledons.

epidermis [Gr. *epi*, upon; *derma*, skin] The outermost layer of cells on a plant body.

epiphyte [Gr. *epi*, upon,; *phyton*, a plant] A plant which grows perched upon other plants.

epithema [Gr. *epi-*, upon; *thēma*, something placed] Water-secreting tissue of a hydathode.

erosion [L. *erodere*, to gnaw away] Wearing land away by the action of ice, wind, and water.

etiolation [French, from L. *stipula*, stubble] Bleaching of plants by exclusion of light.

evolution [L. *evolvere*, to unroll] Hereditary change from generation to generation, producing new forms of living things.

excurrent branching [L. *excurrere*, to run out] A tree form in which there is a main upright trunk from which shorter branches extend outward.

family [L. *familia*] A group of closely related genera.

fat Solid or liquid oil, composed of carbon, hydrogen, and oxygen, the last in smaller proportion than in carbohydrates.

fauna [L. *faunus*, a faun] Animals or animal life as distinguished from the *flora* of a region.

female gametophyte [Gr. *gamein*, to marry; *phyton*, plant] Any gametophyte (haploid plant) which produces eggs.

fertilization [L. *ferre*, to bear or produce] The union of gametes; the formation of a zygote.

fibrous root [L. *fibra*, a thread] A long very slender root, such as those of many grasses; very effective as an absorbing organ.

filament [L. *filamentum*, a thread] The anther-bearing stalk of a stamen; a threadlike series of cells as of an alga or fungus.

Filicineae [L. *filix*, a fern] The class of Pteropsida which includes the ferns.

fire blight A bacterial infection which attacks apples and pears and causes the death of twigs and flower buds. The affected parts appear to be scorched.

F_1: first filial generation [L. *filius*, son] The offspring of a cross between parents which differ in the characteristic or characteristics being studied.

fission [L. *findere*, to split] A simple type of cell division in which the protoplast constricts and finally breaks in two. Characteristic of the Schizophyta. In these plants the cell is the individual, and fission is a primitive form of reproduction.

flagellum (pl. *flagella*) [L. *flagellum*, a whip] A whiplike extension of the cytoplasm of many cells by which they swim or create currents of water.

fleshy fruit A fruit in which all or part of the pericarp is soft and juicy.

flora [L. *flos*, flower] Plants, or plant life as distinguished from the *fauna* or animal life of a region.

florigen [L. *flos*, flower; Gr. *gennān*, to produce] A hormone which brings about the production of flowers.

flower [L. *flos*, flower] The characteristic reproductive structure of angiosperms. One or more stamens or carpels, with or without accessory parts such as perianth, which are instrumental in pollination.

foliose [L. *folium*, a leaf] Attached by a limited area but with margins free from the substratum. (Of flat and somewhat leaf-like lichens.)

follicle [L. *folliculus*, a small bag] A monocarpellary dry fruit which dehisces along one side only.

food Any substance which can be assimilated or used to release energy.

foot A specialized absorbing organ of the embryo sporophyte of ferns and bryophytes, by which food and water are removed from the gametophyte.

formative response [L. *forma*, shape] A response to a stimulus in which the activities or products of plant cells are influenced or altered.

fossil [L. *fodere*, to dig] Any evidence of life which existed in ancient times.

fragmentation [L. *frangere*, to break] A phase of weathering in which the combined effects of both mechanical and solvent activities reduce solid rock masses to smaller and smaller particles.

free nuclear division Mitotic nuclear division which is not accompanied by the formation of cell walls.

fruit [L. *fructus*, enjoyment, fruit] A ripened carpel and its seed or seeds, with or without accessory structures.

fruticose [L. *frutex*, a shrub] Bushy, finely branched. (Of lichens.)

fucoxanthin [Gr. *phykos*, a seaweed; *xanthos*, yellow] A carotinoid which has a rich golden-brown color and is associated with the chlorophyll, carotin, and xanthophyll to form chromatophores characteristic of the brown algae.

fungus (pl. *fungi*) [L. a mushroom] A general term applied to a chlorophyll-deficient thallus plant which possesses cells with organized nuclei.

funiculus (pl. *funiculi*) [L. *funis*, a cord] A short, stalklike structure which connects the ovule of an angiosperm to the placenta and through it to the ovary wall.

gametangium (pl. *gametangia*) [Gr. *angeion*, a container] A cell in which gametes develop.

gamete [Gr. *gamein*, to marry] A sex cell; egg or sperm.

gametophyte generation [Gr. *gamein*, to marry; *phyton*, plant] The haploid or gamete-producing generation of any plant.

gasteromycetes [Gr. *gastēr*, stomach; *mykēs*, fungus] Fleshy fungi with spore-bearing surfaces enclosed by an outer wall, for example, the puffballs.

gemma (pl. *gemmae*) [L., a bud] A mass of slightly organized tissue which functions as a means of vegetative reproduction in many plants, for example, *Marchantia* and *Lycopodium*.

gene [Gr. *geneā*, birth] A determiner of heredity.

generative nucleus [L. *generare*, to beget] A nucleus in the pollen tube which divides, forming two sperm nuclei.

genetic isolation [Gr. *genesis*, origin; L. *insula*, island] Isolation of a group of individuals from the general population by genetic inability to form fertile crosses with the parent stock.

genetics [Gr. *genesis*, origin] The branch of biology which deals with heredity and variation.

genotype ratio [Gr. *genos*, race; *typos*, impression; L. *ratio*, proportion] Relative numbers of offspring in any generation as indicated by their genes. Compare with *phenotype ratio*.

genus (pl. *genera*) [L., race] A category in classification between the species and the family; a group of related species. In a binomial or technical name the genus is the first name and the initial letter is capitalized.

geographic isolation [Gr. *geō-*, earth; *graphein*, to draw; L. *insula*, island] Isolation of a segment of a population from the main body of the group by a geographic barrier such as a mountain range, a river, or an ocean.

geotropism [Gr. *geō-*, earth; *tropē*, a turning] A response to gravity.

Ginkgoales [Japanese, *ginkgo*] An order of gymnosperms, remarkable because the leaves have dichotomous veining (reminiscent of that of ferns) and because the sperms swim. The only living species is *Ginkgo biloba*.

girdleview View of a diatom from the side.

gland [L. *glans*, acorn] An organ of secretion.

glycerol [Gr. *glykys*, sweet] One of the final digestion products of fats, the other being fatty acids. The commercial name of glycerol is glycerin.

glycine [Gr. *glykys*, sweet] The simplest amino acid.

glycogen [Gr. *glykys*, sweet; *gennān*, origin] Animal starch; a polysaccharide found in some of the algae and fungi.

grain [L. *granum*, a seed] The fruit of a grass. See *caryopsis*, *achene*.

grain The texture of wood determined by the kinds of tracheids, vessels, fibers, and rays, together with their arrangements.

Graminales [L. *gramen*, grass] The order to which all grasses belong.

grana [L. *granum*, a grain] Particles of chlorophyll in the stroma of a chloroplast.

growth rings Layers of wood laid down by the cambium in successive periods of growth; commonly the spring and summer wood; applied specifically to the woody stems and roots of gymnosperms and dicotyledons.

growth-regulating substance An auxin; a growth hormone.

guard cell. One of two cells which enclose a stoma.

guttation [L. *gutta*, a drop] Loss of water as a liquid at the ends of veinlets at the tips or along the margins of leaves.

Gymnospermae [Gr. *gymnos*, naked; *sperma*, a seed] The class of seed plants whose seeds are not enclosed in ovaries. The conifers are the best-known examples.

haploid [Gr. *haploos*, simple or single] Having the basic or reduced number of chromosomes.

haustorium (pl. *haustoria*) [L. *haurire*, to drink] The absorbing organ of a parasitic plant.

head An inflorescence made up of many flowers crowded together or on a common receptacle.

heartwood The dark inner part of the wood of a log. The light outer part is the sapwood.

Hepaticae [L. *hepaticus*, the liver] The liverworts.

herbaceous plant [L. *herbaceus*, grassy] A plant which develops little woody tissue, remains succulent, or dies above the ground at the end of each growing season.

heredity [L. *heres*, an heir] The transfer of characteristics from generation to generation.

heteroauxin See *indoleacetic acid*.

heterocyst [Gr. *heteros*, other; *cystis*, a bladder] A specialized cell in filaments of blue-green algae.

heterogamy [Gr. *heteros*, other; *gamein*, to marry] The type of sexual reproduction in which the gametes that unite are unlike in appearance.

heterospory [Gr. *heteros*, other; spore] Having two kinds of spores (microspores and megaspores) in the life cycle.

heterotrophic [Gr. *heteros*, other; *trophikos*, nourishing] Pertaining to organisms or metabolism dependent upon organic material as food, which is either absorbed (fungi) or ingested (animals); organisms unable to produce food from inorganic materials. See *autotrophic*.

heterozygous [Gr. *heteros*, other; *zygon*, yoke] Applied to two genes of an allelic pair that are unlike in the zygote. See *homozygous*.

hilum [L. *hilum*, a trifle] The scar left on a seed where it was attached to the placenta in a fruit.

homospory [Gr. *homos*, the same; spore] Having spores of only one kind.

homozygous [Gr. *homos*, the same; *zygon*, a yoke] Applied to two genes of an allelic pair which are alike in the zygote. See *heterozygous*.

hormogonium (pl. *hormogonia*) [Gr. *hormos*, chain; *-gonos*, progeny] In blue-green algae,

one of a number of simple vegetable fragments which are left when a filament breaks at its heterocysts.

hormone [Gr. *hormain*, to excite] An organic substance which is formed in one part of an organism and functions in trace amounts in another part of that organism, affecting physiological activities, such as growth.

host [L. *hospes*, host] The organism which supplies the food for a parasite.

humus [L., soil] Accumulated debris of partly decayed plant stems, leaves, and roots, forming the organic material in soil.

hybrid [L. *hybrida*, of mixed breed] A cross between parents that differ in at least one characteristic.

hybridization [L. *hybrida*, of mixed breed] Crossing of two unlike individuals; production of hybrids.

hydathode [Gr. *hydat-*, water; *hodos*, way] A water stoma; a pore through which guttation water escapes.

hydric plant [Gr. *hydōr*, water] Water plant; hydrophyte.

hydrolysis [Gr. *hydōr*, water; *lysis*, dissolving] Making soluble by the chemical addition of the elements of water; usually a digestive process.

hydrophyte [Gr. *hydōr*, water; *phyton*, plant] A water plant.

hydrotropic response [Gr. *hydōr*, water; *tropos*, turning] A positive response of roots growing toward the moist side, thus entering the soil that contains the greater amount of moisture.

hygroscopic tissue [Gr. *hygros*, moist; *skopein*, to see] Tissue which changes its shape because of unequal swelling or shrinkage of different parts as they absorb or lose moisture.

hymenium (pl. *hymenia*) [Gr. *Hymēn*, the god of marriage] The spore-bearing surface of a fleshy fungus.

Hymenomycetes [Gr. *Hymēn*, the god of marriage; *mykēs*, fungus] Basidiomycetae with exposed spore-bearing surfaces or hymenia.

hypha (pl. *hyphae*) [Gr. *hyphē*, a web] A threadlike element of a fungus.

hypocotyl [Gr. *hypo*, below; *cotylē*, a cup] The part of an embryo immediately below the cotyledon or cotyledons.

hypodermis [Gr. *hypo*, below; *derma*, skin] Certain cells just inside the epidermis of root or stem which, after the death of the epidermis, undergo changes causing them to form a waterproof layer which reduces both absorption and loss of water.

hypogeous germination [Gr. *hypo*, below; *gē*, the earth] Germination in which the cotyledons remain underground.

I.A.A. See *indoleacetic acid.*

imbibition [L. *imbibere*, to drink] Taking up or absorbing of water by a colloid.

immunization [L. *immunis*, exempt from a tax] Giving an organism the power to resist disease; reaction to a foreign protein.

imprint The surface features of leaves, stems, roots, fruits, and other parts of organisms, recorded in fossils; also called a *mold.*

incomplete dominance In genetics, the condition existing when one allele does not entirely overshadow the other; that is, dominance is not complete.

indehiscent [L. *in-*, not; *dehiscere*, to gape] Not breaking open when mature.

indusium (pl. *indusia*) [L. *induere*, to put on] A covering over a sorus in ferns.

indeterminate inflorescence The type of inflorescence in which the terminal bud is free to grow and enlarge the flower cluster indefinitely.

indoleactic acid or **heteroauxin** An important growth-regulating hormone of plants.

inflorescence [L. *inflorescere*, to begin to bloom] Any grouping of flowers on a plant. There are two types, *determinate* and *indeterminate* inflorescence.

integument [L. *integere*, to cover] An immature seed coat.

intercalary meristem [L. *intercalarius*, inserted] A growing meristematic region, especially above each node in certain plants as grasses, mints, etc.

internode [L. *inter*, between; *nodus*, a knot] The part of a stem between nodes.

interphase [L. *inter*, between; Gr. *phainein*, to show] A nucleus which is not undergoing division is said to be in interphase; *resting nucleus.*

involucre [L. *involucrum*, a covering] A whorl of bracts below a flower cluster.

ion [Gr. *ienai*, to go] An electrically charged organic or inorganic particle.

irritability [L. *irritare*, to cause impatience] The capacity of protoplasm to respond to stimuli.

isogamete [Gr. *isos*, equal] A gamete which appears similar to its mate.

isogamy [*isos*, equal; *gamos*, marriage] The type of sexual reproduction in which isogametes unite.

lamella (pl. *lamellae*) [L., a very thin layer] A gill on the lower side of a gill fungus; a leaf blade.

latex [L., a fluid] Milky fluid produced by certain plants. Rubber and chicle are among the important commercial latex products.

latex vessel A special tube in which latex is produced and located.

leader The upper part of the main vertical shaft of a tree with excurrent branching.

leaf mosaic [Gr. *Mouseios*, of the muses] The pattern formed by leaves as they adjust themselves to light. Also, a virus disease of some plants which prevents normal development of chlorophyll, and thereby produces a mottled appearance.

leaf primordium (pl. *primordia*) [L. *primordium*, beginning] A protuberance a short distance below the tip of a stem, which develops into a leaf.

leaf scar A scar below each axillary bud, left by the breaking away of the petiole of the leaf of the previous season.

leaf trace During abscission, the mark left in the leaf scar by the vascular bundles when they break away from the twig; the vascular tissue extending from stem into leaf.

legume [L. *legere*, to gather] A dehiscent simple fruit which splits along two sides, forming two valves; a peculiar kind of pod characteristic of the pea family, for example, pea, bean, peanut.

Leguminosae [L. *legere*, to gather] The pea family.

lenticel [L. *lenticellus*, a little lens] A cortical pore in a stem or old root.

leucoplast [Gr. *leukos*, white; *plastos*, formed] A colorless plastid in the cytoplasm.

liana A woody vine; any climbing plant rooted in the soil.

lichen [Gr. *leichēn*] A fungus and an alga intimately combined into one body which lives symbiotically.

light requirement The amount of light required by a plant to attain proper growth.

light tolerance The amount of light that a plant can endure and still attain normal growth.

lignin [L. *lignum*, wood] A substance associated with cellulose, and giving it the essential characteristics of wood.

ligule [L. *ligula*, a strap] A more or less definite collarlike extension where the sheath merges with the blade of a leaf of grass.

linear tetrad [Gr. *tetras*, four] In seed plants, the arrangement in a line of a group of four megaspores.

linkage The tendency of certain groups of genes to remain together because they occur on the same chromosome.

lip cell One of two specialized cells opposite the annulus of a fern sporangium and instrumental in discharging the spores.

lipase [Gr. *lipos*, fat; *-ase*, an enzyme] An enzyme which accelerates the hydrolysis of fats, producing fatty acids and glycerol.

liverwort. A bryophyte of the class Hepaticae.

loam. A mixture of sand, clay, and humus in various proportions, organized into a well-balanced soil.

loess [German *lösen*, to release] A type of soil of outstanding fertility, deposited in humid climates as dust carried by wind from distant arid regions.

loment [L. *lomentum*, bean meal] A legumelike fruit constricted between the seeds and breaking crosswise; for example, the beggar tick.

long-day plant A plant which blossoms in nature only in the longest days of midsummer, for example, wheat, lettuce, radish.

lumen (pl. *lumina*) [L., an opening for light] The passageway in a tubular structure; hence a cell wall without protoplasmic contents, for example, tracheids and water tubes.

Lycopsida [Gr. *lykos*, a wolf; *-opsis*, appearance] The group of vascular plants often called *club mosses*.

lysine [Gr. *lysis*, dissolution] A complex amino acid; a component of many proteins.

macrophyllous plants [Gr. *makros*, large; *phyllon*, a leaf] Plants whose stems have leaf gaps and whose leaves have more or less intricate patterns of veins. (See *microphyllus plants*.)

magnesium [Gr. *Magnēsia*, a region in Greece] One of the chemical elements, a part of the chlorophyll molecule.

maltase [Engl. *malt*] An enzyme which accelerates the hydrolysis of maltose, forming glucose.

maltose A disaccharide sugar; a digestion product of starch.

maple-beech forest A mesic forest in which maple and beech act as the dominants.

marl [L. *margila*] A mixture of calcium carbonate with clay. Under certain conditions marl is deposited in ponds.

mechanical tissue Strengthening tissue such as sclerenchyma, collenchyma, and wood fibers.

megasporangium (pl. *megasporangia*) [Gr. *megas*, large; *sporos*, seed; *angeion*, a container] A sporangium producing megaspores.

megasporophyll [Gr. *megas*, large; *sporos*, a seed; *phyllon*, a leaf] A sporophyll which produces megaspores.

meiosis [Gr. *meiōn*, smaller] Reduction division; a peculiar type of nuclear division in which the chromosome number is divided by two.

Mendel's laws of heredity [After the Austrian abbot Gregor J. *Mendel*] Independent genes, dominance, and segregation.

meristem [Gr. *merizein*, to divide] Embryonic or formative tissues of plants.

mesophyll [Gr. *mesos*, middle; *phyllon*, a leaf] The chlorenchyma of a leaf.

mesophyte [Gr. *mesos*, middle; *phyton*, a plant] A plant which thrives best in an environment with a moderate amount of moisture; a mesic plant.

Mesozoic Era [Gr. *mesos*, middle; *zōē*, life] The geologic era between the Paleozoic and the Cenozoic Eras.

metabolism [Gr. *meta ballein*, to change] All the chemical processes in protoplasm; anabolism and catabolism.

metaphase [Gr. *meta*, after; *phainein*, to show] A phase in mitosis following the prophase, in which the split chromosomes are grouped at the equator of the cell.

metaxylem [Gr. *meta*, after; *xylon*, wood] The portion of primary xylem maturing after the protoxylem has formed.

micron [Gr. *mikros*, small] The unit of measure with the microscope, 0.001 mm. or about 0.0025 in., represented by the Greek letter μ.

microphyllous plants [Gr. *mikros*, small; *phyllon*, leaf] Plants, such as the various lycopods, whose stems do not have leaf gaps and whose leaves characteristically have a single unbranched vein.

micropyle [Gr. *mikros*, small; *pylē*, gate] The minute orifice in the integument of an ovule, through which pollen grains or pollen tubes enter. In the mature seed this opening often remains as a passageway through the testa.

microsporangium [Gr. *mikros*, small; *sporos*, a seed; *angeion*, a container] A sporangium which produces microspores.

microspore [Gr. *mikros*, small; *sporos*, a seed] The small spore produced by heterosporous plants which germinates into a male gametophyte.

microsporophyll [Gr. *mikros*, small; *sporos*, seed; *phyllon*, leaf] A sporophyll which bears the microspores.

middle lamella [L. *lamina*, a thin layer] A layer, commonly of pectic material, which cements adjacent cell walls together.

midrib The large vein of a leaf extending the entire length of the blade.

mitosis [Gr. *mitos*, a thread] The nuclear changes that are usually involved in cell division.

mixed bud The organization of both flower and leaf primordia, permitting flowers and leafy shoots to develop together.

mold A fungus which forms a filamentous coating over the material on which it grows; a mildew.

monocotyledon [Gr. *monos*, alone; *kotylēdōn*, cup] A plant with a single cotyledon in the seed.

monoecious [Gr. *monos*, alone; *oikos*, house] Having staminate and pistillate flowers on the same plant; having both male and female reproductive organs on the same individual.

monohybrid [Gr. *monos*, alone; L. *hybrida*, of mixed breed] The product of a genetic cross in which a single set of alleles is considered.

monosaccharide [Gr. *monos*, alone; *sakchari*, sugar] A simple sugar; a hexose ($C_6H_{12}O_6$) such as glucose, or a pentose ($C_5H_{10}O_5$).

morphology [Gr. *morphē*, form; *logos*, discourse] A branch of botany which is the study of the form, structure, and stages in the development of plants.

moss A bryophyte belonging to the class Musci.

multiple fruit A fruit derived from many flowers ripened together, for example, mulberry and pineapple.

Musci [L. *muscus*] Mosses.

mustard family Cruciferae.

mutant [L. *mutare*, to change] A change in the genes, often bringing about a marked phenotypic alteration.

mycelium (pl. *mycelia*) [Gr. *mykēs*, mushroom] The mass of interwoven hyphae that forms the body of a fungus.

Mycophyta [Gr. *mykēs*, mushroom; *phyton*, plant] Fungi.

mycorrhiza [Gr. *mykēs*, mushroom; *rhiza*, root] A root-fungus combination in which hyphae grow between or into the cells of roots.

Myxomycetae [Gr. *myxa*, slime; *mykēs*, fungus] Slime molds.

Nastic response [Gr. *nastos*, pressed close] A response which is not controlled by the direction from which the stimulus comes.

natural pruning The death of twigs that do not receive sufficient light to continue to grow.

natural selection Destruction by natural means of those individuals which are not well adjusted to environment. This selection leaves the better individuals to reproduce their kind and perpetuate their successful characteristics.

neck An extension, containing a canal, from the venter of an archegonium.

nitrate A compound of nitrogen, oxygen, and such basic elements as potassium, sodium, or calcium.

nitrification The oxidation of ammonium compounds to nitrites, and of nitrites to nitrates.

nitrifying bacteria Bacteria which oxidize ammonia and nitrites.

nitrogen fixation The combining of free nitrogen into compounds.

nitrogen-fixing bacteria Bacteria capable of combining free nitrogen into compounds. Found in root nodules of some plants, especially of members of the pea family; also living free in the soil.

node [L. *nodus*, a knot] The part of a stem at which a leaf or bud arises.

nodule [L. *nodus*, a knot] A knoblike enlargement, as on the roots of certain legumes.

nondisjunction [L. *non*, not; *dis*, away from; *jungere*, to join] The failure of a pair of homologous chromosomes to separate during meiosis, thus producing a nucleus otherwise haploid but with one chromosome in duplicate. This behavior causes a divergence from the standard in hereditary features.

nucellus [L. diminutive of *nux*, a nut]. The megasporangium in an ovule.

nuclear membrane [L. *nucleus; membrana*, skin] The thin layer of protoplasm which bounds the nucleus.

nuclear reticulum [L. *nucleus; reta*, a net] The network of chromatin in a resting or interphase nucleus.

nuclear sap The liquid which fills the central vacuole of a nucleus.

nucleolus (pl. *nucleoli*) [L. diminutive of *nucleus*, a kernel] A deeply staining, often rounded body, seen most frequently in resting nuclei.

nucleus (pl. *nuclei*) [L. a kernel, diminutive of *nux*, a nut]. The part of a cell aside from the cytoplasm. It is constructed largely of chromatin and carries the genes.

nut A one-seeded fruit derived from more than one carpel and having a hard, dry, indehiscent pericarp, for example, beechnut, acorn.

nutrient elements [L. *nutrire*, to feed] Chemical elements which take part in metabolism.

nutritive symbiosis [L. *nutrire*, to feed; Gr. *sym-*, with; *bios*, life] Symbiotic relationships in which there is an exchange of food.

oak-hickory association. A plant association in which oaks and hickories are the dominants.

oögonium (pl. *oögonia*) [Gr. *ōion*, egg; *gonos*, offspring] The cell which becomes the egg in algae and fungi.

operculum [L. *operire*, to cover] A lid which covers a moss capsule.

organ [Gr. *organon*, a tool] The part of a plant, made up of tissues, that carries on a special func-

tion or group of functions, for example, root, stem, leaf.

organic substances Carbon compounds. The term originally referred to the products of life activities.

organism Any living individual.

osmosis [Gr. *ōsmos*, impulse] Differential diffusion through a semipermeable or differentially permeable membrane.

osmotic pressure [Gr. *ōsmos*, impulse]. The pressure a solution is capable of producing if placed under suitable conditions; the pressure which results from osmosis.

ovary [L. *ovum*, an egg] The enlarged portion of a carpel or pistil containing one or more ovules.

ovulate cone [L. *ovum*, an egg] The ovule- or seed-bearing cone of a conifer.

ovule [L. *ovulum*, diminutive of *ovum*, egg] An immature seed; the female gametophyte of a seed plant, surrounded by the nucellus and integuments.

ovuliferous scale [L. *ovulum; ferre*, to bear]. The cone scale of a conifer which bears ovules.

oxidase [*-ase*, indicating an enzyme] An enzyme which accelerates oxidation; a respiratory enzyme.

oxidation The union of oxygen with another substance. The removal of hydrogen from a compound is also, in effect, oxidation.

paleobotany [Gr. *palaios*, ancient; botany] The study of plant fossils.

paleontology [Gr. *palaios*, ancient; *onto-*, being; *logos*, discourse] The science which deals with the life of ancient geologic periods.

Paleozoic Era [Gr. *palaios*, ancient; *zōē*, life]. The geologic era preceding the Mesozoic Era.

palisade tissue [L. *palus*, a stake] Mesophyll cells that elongate at right angles to the epidermis.

palmate [L. *palmatus*, hand-shaped] A type of leaf venation and compounding in which the veins or leaflets all radiate from the summit of the petiole, for example, buckeye, clover.

panicle [L. *panus*, a tuft] A compound raceme, i.e., one in which the lateral branches are also racemose in form.

paraphysis (pl. *paraphyses*) [Gr. *para*, beside; *physis*, growth] One of the sterile, slender filaments commonly borne among the spore-bearing organs of the lower plant groups.

parasite [Gr. *parasitos*, eating at the table of another] An organism which takes food from a living plant or animal.

parasitism Nutritive symbiosis in which one symbiont takes food from the other.

parenchyma [Gr. *para*, beside; *en-*, in; *chein*, to pour] A tissue composed of living, thin-walled cells that are well supplied with intercellular spaces.

parthenocarpy [Gr. *parthenos*, a maiden; *karpos*, fruit] The production of fruit without fertilization.

parthenogenesis [Gr. *parthenos*, a maiden; *genesis*, origination] Reproduction in which an unfertilized egg develops as if it were a zygote.

pathology [Gr. *pathos*, disease; *logos*, discourse] The branch of biology which deals with diseases.

pectin [Gr. *pēktos*, congealed] A jellylike polysaccharide which commonly acts as a middle lamella (layer of cementing material) between the walls of adjacent cells. Pectin tends to take up water and become gelatinous under certain conditions.

pedicel [L. *pedicellus*, a little foot] A slender stalk supporting a flower or fruit.

peduncle [L. diminutive of *pes*, foot]. The main stalk of a compound inflorescence.

Pennsylvanian Period A Paleozoic period between the Mississippian and the Permian; often called Upper Carboniferous.

pepo [L. *pepo*, a melon] The characteristic fruit of the gourd family.

pepsin [Gr. *pepsis*, digestion] A proteolytic enzyme.

peptidase [Gr. *pepsis*, digestion; *-ase*, enzyme] An enzyme of the protease group which further digests the polypeptides, breaking them down into amino acids.

perennial [L. *per*, through; *annus*, year] Continuing to live from year to year.

perfect flower A flower with both stamens and pistil.

perianth [Gr. *peri*, around; *anthos*, flower] Petals and sepals taken collectively.

pericarp [Gr. *peri*, around; *karpos*, a fruit] The ripened walls of the ovary.

pericycle [Gr. *peri*, around; *kyklos*, circle] The outside layer of the stele.

periderm [Gr. *peri*, around; *derma*, skin] The cork layer which covers the mature stem and root.

periodicity The seasonal behavior of flowering plants. The three types of photoperiodicity are short-day, long-day, and neutral or indifferent.

peristome [Gr. *peri*, around; *stōma*, mouth] the teeth around the mouth of a moss capsule.

petal [Gr. *petalos*, a leaf] A leaf-like segment of the flower just inside the sepals. It is often highly colored and presumably attracts insects.

petiole [L. *petiolus*, a little foot] The stalk of a leaf.

petrification [L. *petra*, a stone; *facere*, to make] The changing of organisms into stone by infiltration.

Phaeophyta [Gr. *phaios*, dusky; *phykos*, a seaweed] Brown algae.

phenotype [Gr. *phainein*, to show; *typos*, impression] The visible and measurable characteristics of a hybrid.

phenotype ratio The relative numbers of offspring in any generation as determined by physical appearance independent of their genetic make-up. Compare with *genotype ratio*.

phloem [Gr. *phloos*, bark] The food-conducting tissue of the stele of higher plants, constructed largely of sieve tubes, companion cells, and phloem parenchyma.

phloem ray A ray continuous with a xylem ray and extending through the cambium.

photoperiodicity [Gr. *phōs*, light; *periodus*, going around] Seasonal, light-regulated activity, such as flowering and vegetative growth of plants.

phototaxis [Gr. *phōs*, light; *tassein*, to arrange] Sensitiveness and response of a free-moving organism to the direction of light.

phototropism [Gr. *phōs*, light; *tropē*, a turning] A bending or turning in response to light.

phycocyanin [Gr. *phkyos*, a seaweed; *kyanos*, dark blue] The blue pigment responsible in part for the color of blue-green algae.

phycoerythrin [Gr. *phykos*, seaweed; *erythros*, red] A red pigment characteristic of the red algae; sometimes also found in blue-green algae.

Phycomycetae [Gr. *phykos*, seaweed; *mykēs*, fungus] The class of algalike fungi.

phylum [Gr. *phylon*, tribe] (In botany, the word *division* is used as a synonym for phylum.) The largest classification unit; a group of classes, for example, Bryophyta, Pteropsida.

physiologic dryness [Gr. *physis*, nature; *logos*, discourse] A situation that occurs under certain conditions, in which ample water is present but is available to plants in only limited amounts; for example, frozen soil or water containing high concentrations of dissolved minerals.

physiology [Gr. *physis*, nature; *logos*, discourse] That branch of biologic science which deals with the functions of organs, the actions of enzymes, etc., including respiration, the acquisition of food, and growth.

pileus [L. *pileus*, a cap] The cap of an umbrella-type fungus.

pinnate [L. *pinna*, feather] Having a featherlike type of venation or leaf composition in which all leaflets or veins extend outward from a common midvein or rachis which serves as a line of origin. The leaf of the locust is an example of a pinnately compound leaf.

pioneer species The first successful plant invaders of an uninhabited location.

pistil [L. *pistillum*, a pestle] The ovule-bearing organ of a flower; carpel.

pith The soft inner portion of a stem, root, or leaf in vascular plants; parenchyma, or ground tissue.

pitted vessel A xylem element with thin places, or pits, in the walls.

placenta [L. *placenta*, a cake] The portion of the ovary of an angiosperm to which the ovules are attached.

plankton [Gr. *planktos*, wandering] Organisms, usually of microscopic size, suspended or swimming in the water.

plant association A community in which one or more species, known as *dominants*, play important roles in changing or controlling the environment.

plant community All the plants growing in a given habitat; an organized plant association.

plant ecology [Gr. *oikos*, house; *logos*, discourse] The science of plants as they are related to their environment.

plasma membrane [Gr. *plassein*, to mold] The thin layer of cytoplasm which is the outer

boundary of a cell. It is usually firmly pressed against the wall.

plasmodesma (pl. *plasmodesmata*) [Gr. *plasma; desma*, a bond] Protoplasmic connections through pits in the walls of adjoining cells.

plasmodium [Gr. *plasma; eidos*, form] A soft, slimy mass of protoplasm which constitutes the animal-like phase in the life cycle of a slime mold.

plasmolysis [Gr. *plasma; lysis*, loosening] The shrinking of the cytoplasm of a cell.

plastid [German from Gr. *plastos*, formed] A specialized particle of cytoplasm.

plumule [L. diminutive of *pluma*, a feather] The epicotyl of a seed or seedling. The embryonic shoot. In a few plants, such as the bean, the epicotyl has a somewhat featherlike appearance.

pollen [L. *pollen*, dust] The male gametophytes of seed plants.

pollen sac [L. *pollen*, dust; *saccus*, sack] Microsporangium wall of a seed plant.

pollination Transfer of pollen from stamen to stigma or ovule.

polyploid [Gr. *polys*, many; *ploos*, fold; *eidos*, form] Having more than two sets of chromosomes.

polysaccharide [Gr. *polys*, many; *sakchari*, sugar] A complex carbohydrate such as starch, cellulose, or pectin, composed of numerous monosaccharide submolecules.

pome [L. *pomum*, a fruit] An applelike fruit.

pond successions [L. *succedere*, to follow] The series of associations which normally follow one another in a pond.

population pressure Crowding due to overproduction of offspring.

prickle A sharp outgrowth from the superficial tissues of a stem or leaf, for example, rose, blackberry.

primary permanent tissues [L. *primus*, first; *permanere*, to remain] The permanent tissues derived from apical meristems.

primary root [L. *primus*, first] The embryonic root, commonly the first structure to elongate into the soil when germination takes place.

primary xylem [L. *primus*, first; Gr. *xylon*, wood] The xylem which is derived from procambium.

procambium [Gr. *pro*, before; L. cambium, exchange] The precursor of primary xylem and phloem.

proembryo [Gr. *pro*, before; *embryein*, to expand]. The early stages in a developing embryo of a seed plant.

propagule [L. *propagare*, to propagate; *-ule*, a diminutive] Any organ of propagation.

prophase [Gr. *pro*, first; *phainein*, to show] The change in the nucleus, from the resting stage (interphase) to the metaphase, in which the chromosomes have become fully formed and are longitudinally split but the chromatids still remain side by side.

prosthetic group [Gr. *prosthesis*, an addition] The part of an enzyme which acts with the protein fraction of the enzyme to bring about a metabolic change.

protease [*protein; -ase*, enzyme]. A protein-digesting enzyme.

protein [Gr. *prōteios*, primary] One class of compounds essential to all living things and made up of amino acids, chiefly composed of carbon, oxygen, hydrogen, nitrogen, and sulfur.

Protochlorophyta [Gr. *prōtos*, first; *chloros*, green; *phyton*, plant] Green algae; primitive green plants.

protonema [Gr. *prōtos*, first; *nēma*, thread] The early filamentous stage in the development of a moss gametophyte.

protoplasm [Gr. *prōtos*, first; *plasma*, thing formed] Living substance; the substance from which cells are organized.

protoplast [Gr. *prōtos*, first; *plastos*, made] The protoplasm of a single cell.

protostele [Gr. *prōtos*, first; *stēlē*, a post] A stele in which the xylem occupies the central position, for example, roots and stems of certain primitive plants.

protoxylem [Gr. *prōtos*, first; *xylon*, wood] The first xylem cells to be organized from procambium in a developing root, stem, or leaf.

Psilopsida [Gr. *psilos*, bare; *opsis*, appearance] The most primitive group of vascular plants.

pteridophyte [Gr. *pteridos*, a fern; *phyton*, plant] A vascular plant in which sporophyte and gametophyte are physiologically independent at maturity.

Pteropsida [Gr. *pteron*, feather; *opsis*, appearance] The division which includes the ferns and the modern seed plants.

pulvinus (pl. *pulvini*) [L. *pulvinus*, a cushion] In some plants, a special organ acting as the agent of motion which causes leaves to fold quickly.

pyrenoid [Gr. *pyrēn*, a fruit stone; *eidos*, form] A cell structure in algae, in or on chloroplasts, serving as a center for starch formation.

raceme [L. *racemus*, a bunch of berries] A type of inflorescence in which the elongating axis bears flowers on short pedicels in succession toward the apex.

rachis [Gr., *spine*] Axis of a compound leaf.

radical [L. *radix*, a root] A group of atoms which acts as a unit.

ramentum [L. *radere*, to scrape] The chaffy scales which usually clothe the base of a fern petiole; one of the superficial characteristics used in distinguishing ferns from other plants.

raphe [Gr. *raphē*, a seam] A long slit in the wall of the valve of a diatom.

ray [L. *radius*] A part of the conductive system of plants which transfers water from the xylem and food from the phloem across the stem or root to any cells that may be somewhat distant from the source of supply.

receptacle [L. *recipere*, to receive] The end of a floral stem to which the calyx and corolla are attached.

recessive [L. *recedere*, to recede] A gene suppressed by its allele.

reductase [L. *reducere*, reduce; *-ase*, an enzyme). An enzyme which removes oxygen or one which adds hydrogen.

reduction division Meiosis; nuclear division in which the chromosome numbers are divided by two.

resin (also **rosin**) [Gr. *rhētinē*] The raw sap produced in the conifers and to a certain extent in other plants.

resin duct [L. *ducere*, to lead] A glandular tube where resin is produced and stored, common in conifers.

respiration [L. *respirare*, to breathe] The release of energy in the protoplasm, usually by means of oxidation.

respiratory enzymes The oxidases.

resting cell In some algae, an occasional cell which, after becoming gorged with food and enlarged slightly, forms a thick wall and remains dormant, often remaining viable for many years: akinete.

rhizoid [Gr. *rhiza*, root; *eidos*, form] One of the filaments which attach the gametophyte of mosses, liverworts, and ferns to the substratum.

rhizome [Gr. *rhizoma*, a mass of roots] An underground stem.

Rhodophyta [Gr. *rhodo*, rose; *phyton*, plant] Red algae.

root cap The protective covering on the tip of a root.

root hair An outgrowth of an epidermal cell of the root, specializing in absorption of water and dissolved minerals.

root pressure The pressure in a root caused by osmotic movement of water to all the cells of the root.

runner A slender, prostrate stolon; a stem extending horizontally on the surface of the soil and taking root at the end or at the nodes.

rust A pathogenic basidiomycete of the order Uredinales, frequently having reddish spores similar to iron rust in color.

samara [L. *samara*, an elm seed] A winged fruit, for example, ash, elm, maple.

saprophyte [Gr. *sapros*, rotten; *phyton*, plant] A plant living on dead or decaying organic matter.

saprophytic bacteria All bacteria whose digestive activities bring about the decay of the materials in which they grow. They are dependent for food on organic materials from sources outside themselves and secrete enzymes that digest nonliving plant and animal bodies.

sapwood The outer cylinder of a tree's woody stem, immediately surrounding the heartwood and gradually changing into it as growth progresses.

scalariform vessel [L. *scala*, a ladder] A water tube or tracheid with transverse pits, somewhat resembling a ladder.

scape [L. *scapus*, stalk] A peduncle which rises from the ground and has no true foliage leaves, for example, most violets, the dandelion, and the lily of the valley.

scattered stele [Gr. *stēlē*, post] A stele in which the parts, or vascular bundles, are arranged in no regular pattern, for example, monocotyledon stems.

Schizomycetes [Gr. *schizein*, to split; *mykēs*, fungus] Bacteria.

Schizophyta [Gr. *schizein*, to split; *phyton*, plant] Fission plants; the bacteria and blue-green algae.

sclereid [Gr. *sklēros*, hard] A stone cell; a short, often irregularly shaped, lignified cell wall; for example, shells of nuts are composed of sclereids.

sclerenchyma [Gr. *sklēros*, hard; *enchyma*, something poured in] Lignified mechanical tissue of the phloem or cortex.

sclerotium (pl. *sclerotia*) [Gr. *sklēros*, hard] Hardened mycelium of certain parts of fungi.

secondary phloem [Gr. *phloios*, bark] Phloem produced by the cambium.

secondary root One of the roots arising from the embryonic primary root; a root branch.

secondary succession [L. *succedere*, to follow] A succession, or sere, which follows destruction or disturbance of a biome or association.

secondary tissue A tissue produced by cambium.

secondary xylem Xylem produced by the cambium.

Secretion [L. *secernere*, to separate] A substance produced by glands.

seed A more or less dormant embryo sporophyte enclosed in a nucellus which is encased in a testa.

segregation [L. *segregare*, to separate] The separation of allelic genes during meiosis.

self-pollination [L. *pollen*, dust] The transfer of pollen from an anther to a stigma on the same plant, whether within the same flower or not.

sepal [Gr. *skepē*, cover] A division of the calyx.

septate [L. *septum*, a fence] Divided by cell walls.

seral Of a sere.

sere [L. *serere*, to follow] A succession of ecological communities. Each modifies the conditions in such a manner that other associations follow.

sessile [L. *sedere*, to sit] Unattached to a peduncle or a stalk but attached directly by the base.

seta (pl. *setae*) [L. *seta*, a bristle] In certain plants, a slender stalk which is topped by the capsule.

sexual reproduction Reproduction by means of gametes.

sheath A thin structure in grasses that enwraps the stem and from which the blade arises.

short-day plant A plant which blossoms only in spring or fall when days are short, for example, certain asters and chrysanthemums.

short-grass association An ecological association in which low-growing grasses are the dominant species.

shrub A woody plant smaller than a tree and usually more profusely branched than a tree, for example, roses, lilacs, and blackberries.

sieve plate A perforated portion of a wall which separates two cells that fit together end to end, by means of which rows of cells form long sieve tubes. The sieve plate is the most conspicuously visible characteristic of a sieve cell.

sieve tube A tube formed of a series of conducting cells of the phloem.

siphonostele [Gr. *siphōn*, tube; *stēlē*, post] A stele with a central pith.

slime molds Myxomycetae.

social symbiosis Symbiosis in which there is no exchange of food.

sod. A combination of branching rhizomes and numerous adventitious fibrous roots growing from them.

soil profile [L. *pro*, forth; *filum*, a thread] All the layers of soil taken together as a unit.

solution [L. *solvere*, to loosen] A system in which molecules or atoms of a solid, a liquid, or a gas are dispersed as solutes in a liquid solvent from which they may be recovered by crystallization or other physical processes.

solvent [L. *solvere*, to loosen] The liquid in which another substance is dissolved.

soredium (pl. *soredia*) [Gr. *sōros*, a heap] A special reproductive structure which separates from the surface of a lichen. Each soredium is a particle made up of a few algal cells entangled with fragments of fungal hyphae.

sorus (pl. *sori*) [Gr. *sōros*, a heap] In ferns, a cluster of sporangia on the underside of ordinary foliage leaves or on somewhat specialized leaves or leaflets.

spathe [Gr. *spathē*, blade] A showy bract attached below the fleshy floral axis (spadix) of members of the Araceae, for example, the calla lily and jack-in-the-pulpit.

species (pl. *species*) [L., a kind] The smallest usual classification unit; a group of plants or animals

having a common origin, showing more or less similarity to one another, and interbreeding freely with one another but not with individuals of other species.

spectroscope [*spectrum;* Gr. *skopos*, viewer] An optical instrument which analyzes light by separating it into its component rays.

spectrum [L., image] A band of seven colors which together make up white light.

sperm [Gr. *sperma*, seed] A male gamete.

sperm nucleus One of two nuclei resulting from a mitotic division of the generative nucleus of a seed plant.

spermatium (pl. *spermatia*) [Gr. *sperma*, a seed] A very small, sporelike cell produced in the spermogonium of a rust fungus and functioning as a sex cell. By way of a trichogyne it brings about fertilization, initiating the production of an aecium.

spermatophyte [Gr. *sperma*, seed; *phyton*, a plant] A seed plant.

spermogonium (pl. *spermogonia*) [Gr. *sperma*, seed; *gonos*, offspring] A flask-shaped cavity in which spermatia are produced.

Sphenopsida [Gr. *sphēn*, wedge; *opsis*, appearance] The horsetails and scouring rushes and related fossil groups.

spike A type of indeterminate inflorescence which is much like a raceme with the exception that the flowers are sessile on the main axis, for example, plantain and verbena.

spindle A microscopic figure composed of cytoplasmic fibers, *spindle fibers*, on which chromosomes are arranged during nuclear division.

spine [L. *spina*] A sharp modified leaf or part of a leaf.

spiral vessel A water tube which has spiral woody bands within its walls.

spirillum (pl. *spirilla*) [L. diminutive of *spira*, a coil] A spiral or corkscrew-shaped bacterial cell.

spongy mesophyll [Gr. *mesos*, middle; *phyllon*, leaf] The spongy tissue of a leaf.

sporangiophore [*sponangium;* Gr. *pherein*, to bear] A stalk bearing a sporangium.

sporangium (pl. *sporangia*) [Gr. *sporos*, a spore; *angeion*, a container] A spore case.

spore [Gr. *speirein*, to sow] A one-celled or few-celled reproductive structure other than a gamete or zygote. The term is sometimes applied to resting cells of bacteria and blue-green algae.

spore mother cell A sporophyte cell which is capable of undergoing meiosis and producing a tetrad of haploid spores. These normally give rise to gametophytes.

sporogenous [*spore;* Gr. *genesis*, origin] Spore-producing.

sporophore [*spore;* Gr. *pherein*, to bear] A spore-producing body of a fungus, also called a *sporocarp*.

sporophyll [*spore;* Gr. *phyllum*, leaf] A specialized leaf where the sporangia are borne.

sporophyte [*spore;* Gr. *phyton*, plant]. The diploid spore-producing generation of a plant.

stamen [L. *stamen*, a thread] A microsporophyll of a flower; filament and anther; the pollen-bearing part of a seed plant.

staminate cone A gymnosperm cone which bears the microspores or pollen grains.

standard [Old French *estandert*, a banner] The large upper petal of the flower of the pea, often entirely enclosing the remaining four petals before the bud opens.

starch [Old English *stearc*, stiff] A complex carbohydrate; a polysaccharide; the most common form of food storage in plants.

starch sheath The endodermis when its cells contain heavy deposits of starch.

stele [Gr. *stēlē*, a post] The portion of a root, stem, or leaf in which the vascular tissues are found.

stem A stem, as distinguished from a root, has nodes and internodes and either rudimentary or well-developed leaves. The main functions of a stem are the support of the leaves and buds. It is the channel through which water, food, and growth substances travel between the leaves, roots, and fruits.

sterigma (pl. *sterigmata*) [Gr. *sterigma*, support] A slender stalk which supports a basidiospore.

stigma (pl. *stigmata*) [Gr. *stigma*, a spot] In an angiosperm, the special portion of a carpel on which pollen germinates.

stimulus (pl. *stimuli*) [L., goad] Any condition or environmental factor which brings about activity on the part of the protoplasm.

stipe [L. *stipes*, a stalk] The stalk of an umbrella type of mushroom.

stipule [L. *stipula*, a small branch] One of two appendages near the base of the leaf of certain plants.

stolon [Gr. *stolē*, a shoot] An aboveground stem which brings about vegetative propagation.

stoma (pl. *stomata*) [Gr. mouth] A pore through the epidermis.

strobilus (pl. *strobili*) [Gr. *strobilos*, a cone] A cone; a group of sporophylls.

style [L. *stylus*, a writing instrument] A more or less elongated structure between the ovary and the stigma.

subdominants [L. *sub*, under; *dominus*, master] The animals and plants of secondary importance in a biotic community.

suberin [L. *suber*, cork] The waterproof mixture of substances which characterizes cork.

subsoil [L. *sub*, under; *solum*, the ground] A thick stratum of weathered material, sometimes clay, just below the surface layer of soil.

substratum [L. *sub*, under; *sternere*, to spread] The material on which saprophytes grow and from which they get nourishment; the surface on which a lichen grows.

succession [L. *succedere*, to follow] The series of steps by which one plant association follows another in more or less regular order after an alteration in some important phase of the environment.

succulent [L. *succus*, juice] A soft or juicy plant.

suspensor [L. *sub*, below; *pendere*, to hang] An elongating cell of the proembryo which drives the young embryo of a seed plant deep into the tissues of the female gametophyte or endosperm.

symbiont [Gr. *sym*, with; *biōn*, living] One of two participants in symbiosis.

symbiosis [Gr. *sym*, with; *bios*, life] The living together in a more or less definite relationship of two dissimilar organisms.

synergids [Gr. *syn*, with; *ergon*, work] Two of the three cells at the micropylar end of the embryo sac of an angiosperm ovule. The third cell is the egg.

tactic response [Gr. *tassein*, to arrange; L. *respondere*, to answer] A response occurring in free-swimming organisms and in certain specialized swimming cells of complex plants which travel toward or away from some stimulus.

tap root The primary root, when it is large, penetrates deep into the soil, and has few or no large branches.

tapetum [Gr. *tapēs*, a carpet] A layer of nutritive tissue in a sporangium.

taxonomy [Gr. *taxis*, order; *nomos*, law] The division of biology which treats of the orderly naming and classification of organisms; in reference to plants, it is also called *systematic botany*.

teliospore [Gr. *teleios*, final; *spore*] A spore producing a basidium in the telial phase of rust fungi.

telophase [Gr. *telios*, end] The final phase in mitosis.

tendril [L. *tendere*, to stretch] A specialized outgrowth from a stem or leaf which coils around any available support.

tension zone [L. *tendere*, to stretch] The zone of overlap where two plant associations meet; accordingly, some members of each may be found within the bounds of the other.

terminal bud scar [L. *terminare*, to limit] The scar remaining after the scales covering a terminal winter bud have fallen away.

testa (pl. *testae*) [L., an earthenware vessel] A seed coat.

tetrad [Gr. *tetras*, four] A set of four spores produced by one spore mother cell.

tetraploid [Gr. *tetra-*, four; *ploos*, fold; *eidos*, form] Having four sets of chromosomes.

tetraspore [Gr. *tetra*, four; *spore*] Haploid spores in groups of four, produced meiotically by a diploid plant.

thalloid [Gr. *thallos*, a young shoot; *eidos*, form] Pertaining to a *thallus*, which is a plant body only slightly differentiated into organs or tissues.

thallophyte [Gr. *thallos*, a young shoot; *phyton*, a plant] A plant with a body composed of one or many cells or a few tissues, but not differentiated into organized leaf, stem, and root, for example, algae and fungi.

thallus [Gr. *thallos*, a young shoot] A plant body composed of not more than a few tissues and without definite complex organs, for example, algae and fungi.

thigmotropism [Gr. *thigma*, touch; *tropein*, to turn] A response to contact.

thorn A modified branch which is hard and sharp at the outer end.

timberline The line or zone in high mountains above which trees do not grow.

tissue [L. *texere*, to weave] A group of cells of similar origin, structure, and function.

tonoplast [Gr. *tonos*, strain; *plastos*, formed] Vacuolar membrane.

tracheid [Gr. *tracheia*, windpipe] A xylem element derived from one cell.

transfusion cells [L. *trans*, across; *fundere*, to pour] Certain cells of the endodermis of a root, which form opposite the ends of the rays of xylem; also called *passage cells*. Unlike other endodermis cells, the transfusion cells have no suberized thickenings on their walls. Their specialized function is as yet undecided.

transpiration [L. *trans*, across; *spirare*, to breathe] The evaporation of water from the tissues of a plant.

trichogyne [Gr. *tricho-*, a hair; *gynē*, a female] The elongated tubelike upper part of the oögonium or carpogonium of a red alga, basidiomycete, or ascomycete, through which a sperm passes into the oögonium where the nucleus unites with that of the egg, forming the zygote.

trichome [Gr. *trichōma*, hair] A plant hair. These outgrowths are common on many leaves and stems.

triploid [Gr. *triploos*, threefold; *eidos*, form] Having the $3n$ number of chromosomes.

tropism [Gr. *tropos*, turn] The response of a plant organ to external stimuli, especially by growth curvature. The response is *positive* if the structure turns toward the stimulus and *negative* if it turns away.

tube nucleus [L. *tubus*, tube] One of two important nuclei remaining after nuclear division in the male gametophyte of seed plants. It usually remains in the pollen tube.

tuber [L. *tuber*, a *knot*] An underground stem so specialized that it serves as an organ of food storage and reproduction, for example, the white potato.

tumbleweed A type of nearly spherical plant, abundant on the plains, which at maturity breaks off at the ground when shaken by the wind and scatters its seedlike fruits as it goes bouncing across the land.

turgid [L. *turgere*, to swell] Applied to a cell or tissue distended in the process of osmosis.

turgor pressure [L. *turgere*, to swell; *premere*, to squeeze] The stretching of the membrane of a cell in osmosis.

umbel [L. *umbella*, umbrella] A type of inflorescence in which the pedicels are all attached to the summit of the main axis, for example, parsnip, carrot, dill, and water hemlock.

urediniospore [L. *uredo*, *blight*] One type of spore in the rust fungi, produced in the uredinial phase, which infects only a wheat plant or some closely related grass, especially when the weather is moist.

vacuole [L. *vacuus*, empty] A cavity in the protoplasm of a cell, usually filled with cell sap.

vacuolar membrane A layer, similar to the plasma membrane, which lines a vacuole.

valve view [L. *valva*, doorleaf] View of a diatom as seen by the observer looking down on the top of a valve.

variation [L. *variare*, to vary] The fact that no two individuals, plant or animal, are exactly alike (even those having the same parentage), due to two types of cause, heredity and environment.

vascular bundle [L. *vas*, a vessel] A strand of specialized conductive tissues which consist in part of xylem and in part of phloem.

vascular ray One of the xylem and phloem rays.

vascular tissue Conductive tissue.

vein [L. *vena*] A *vascular bundle* of a leaf.

velamen [L. *velare*, to cover] In some of the orchids, a loose, porous, spongelike coating, formed of a highly specialized epidermis, which absorbs and holds large quantities of water.

venation [L. *vena*, vein] The pattern formed by the veins in a leaf.

venter [L., belly] The thick base of an archegonium containing an egg.

ventral canal cell A small, cone-shaped cell above the egg in the upper part of the venter of an archegonium.

vernation [L. *vernare*, to be verdant] The type of arrangement of developing leaves within a bud.

vitamin [L. *vita*, life; *amine*, amino compound] Any one of several organic substances necessary in minute quantities for the development, growth, and proper functioning of plant and animal organs.

volva [L., womb] A cuplike structure in which the stipe is set in some species of gill fungi.

water table The level at which the soil is completely saturated with water.

whorl A circle of structures such as petals or sepals in a flower; the leaf arrangement of a plant in which three or more leaves have their junction at one node on the stem.

wing On the flower of the pea, one of two petals (one on either side) just below the standard; a thin extension from the surface of a seed or fruit.

winged seed A seed which plays the same part in the distribution of a species as a winged fruit, the only difference being that, in the case of seeds, the parachute is an outgrowth of the testa, whereas in the case of a fruit, it develops from the ovary wall.

wood The supporting cells of higher plants, constituting the bulk of the root and stem of trees, shrubs, and lianas; technically, *xylem*.

xanthophyll [Gr. *xanthos*, yellow; *phyllon*, a leaf] A yellow pigment composed chemically of hydrogen, carbon, and oxygen; one of the carotinoids.

xerophyte [Gr. *xeros*, dry; *phyton*, plant] A plant which thrives in dry or exposed places.

xylem [Gr. *xylon*, wood] The water-conducting portion of the stele; wood.

xylem ray One of the platelike layers of cells forming the lines or strips extending outward from the center of a stem or root, the function of which is usually considered to be the transfer of foods and water from cell to cell across the xylem, with occasional temporary storage of starch.

zonation [Gr. *zōne*, a belt] Series of zones of plants, occurring in places where local conditions vary markedly in a short distance, for example, around a shallow lake margin.

zoöid [Gr. *zōion*, an animal] A vegetative, flagellated cell, usually of a colonial alga, such as a cell of *Volvox*.

zoöspore [Gr. *zōion*, an animal] A swimming spore.

zygote [Gr. *zygōtos*, yoked] A fertilized egg; also, the cell resulting from the union of isogametes.

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